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THE PRIMATE BASIS OF HUMAN SEXUAL BEHAVIOR

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HUMAN sexual behavior is ordinarily regarded as a subject that can be understood from the study of man alone. More than that, the prevailing practice of investigators, with few exceptions, has been to regard this behavior, alike in its "normal" and "abnormal" aspects, as something specifically human, in the sense of something that differs radically from the behavior of all non-human mammals. To writers who follow this course a full and clear recognition of man's supposedly isolated psychological position has naturally appeared to be the foundation of all sound reasoning about human activities in the domain of sex, whether in the limited field of sex as the determinant of personal conduct or in the broad field of sex as the starting point for the social institutions that have grown up around it.

This belief that human sexual behavior is governed by its own laws was clearly and simply expressed by Thomas (1909, p. 531) in the words: "But as he [man] came into possession of a characteristic human mind . . . . he began to make the sexual interest a play interest, and this animals have never done. They have a pairing season, and man has not." Thomas did not attempt to tell why or how it has been possible for man thus to deviate from the course pursued by other mammals. He was content with having stated the supposed fact of man's unique attitude toward sex. Bronislaw Malinowski, however, has tried to explain this attitude on physiological grounds. In his first study of Trobriand Island family life (1927, pp. 193–201) he thus contrasts the factors that he believes to regulate the behavior of man's nearest mammalian relatives on the one hand and of man himself on the other:

> Among apes the courtship begins with a change in the female organism, determined by physiological factors and automatically releasing the sexual response in the male. . . . . Mating occurs as the culminating act of courtship and with this the female conceives. With impregnation the rut is over and with its end there ceases the sexual attractiveness of the female. . . . . Outside the rutting season the sexual interest is in abeyance and the competition and strife as well as the overpowering absorption in sex are eliminated from the ordinary life of an animal species.
>
> There is nothing in man which acts with the same sharp determination as does the onset of ovulation in any [other] mammalian female. . . . . man is ready to make love at any time and woman to respond to him—a condition which, as we all know, does not

simplify human intercourse. . . . . The [human] sexual impulse is not confined to any season, not conditioned by any bodily process, and as far as mere physiological forces are concerned, it is there to affect at any moment the life of man and woman . . . . : there is no purely biological release mechanism in man; but instead there is a combined psychological and physiological process determined in its temporal, spacial, and formal nature by cultural tradition . . . .

The views thus expounded by Thomas and by Malinowski are neither new nor are they peculiar to these two writers. It would probably be futile to try to find when and where they first appeared in print, or to try to catalogue all the authors who have, in one form or another, set them forth. They are, indeed, essentially folk beliefs that originated in the popular mind as the result of uncritical comparisons of the ways of men with the obviously different ways of cattle, goats, sheep, deer, swine, horses, and dogs. And, on the sole basis of these comparisons the generally accepted conclusions appear to be well founded; it is unquestionably true that between human sexual behavior and the corresponding behavior of the most widely known mammals other than man great differences exist. It should not surprise any one, therefore, to find how strongly, even in the technical literature of psychology and anthropology, the idea of man's essential peculiarity is intrenched.

When, however, we cease to compare man's behavior merely with that of domestic ungulates and carnivores or with that of imaginary apes acting like partly humanized dogs, and take the trouble to compare it with the true behavior of mammals in general, we find that there is nothing very exceptional in its nature. In this department of his psychology, exactly as in his anatomy and physiology, man is then seen to occupy a definite and easily understood place among the members of the animal class to which he pertains.

In writing this paper I have had two main purposes: *first* to show as clearly as is now possible how the sexual behavior of man is related to that of other mammals, and *second* to discuss more fully than on a previous occasion (Miller, 1928) some of the social implications that seem to arise from the conditions at present known to exist.

THE MAIN TYPES OF MAMMALIAN SEXUAL BEHAVIOR

That all mammals are not subject to a single, uniform rule of sexual behavior is a commonplace of popular observation. For instance, everyone who has paid attention to the breeding habits of mammals knows that the northern members of the deer tribe, with their conspicuous autumnal rutting season, behave differently from domestic cattle and dogs, in which no season of this kind occurs. Unfortunately, in the field of accurately observed animal psychology our knowledge is still very imperfect. But in spite of this circumstance it now seems possible to recognize that the sexual activities of every species of mammal tend to follow the outline of one or the other of three main patterns of behavior. These three patterns or types, which were recognized in part by Heape (1900), are probably dependent on physiological differences in the production of the chemical substances (hormones) that stimulate sexual activity. For the present, however, they can be most conveniently defined in terms of behavior, as follows:

Type No. 1.—Mating behavior of both sexes limited to short, definitely determined periods that are in most instances seasonal in their occurrence. Examples,—many deer and other (though not all) ungulates, most (perhaps all) pinnipeds, some carnivores, some rodents, some bats, and probably most insectivores.

Type No. 2.—Mating behavior of females limited to short, definitely determined periods that may or may not be seasonal in their occurrence; mating behavior of males not thus limited, but always ready to manifest itself in response to a female in appropriate physiological condition. Examples,—all of our familiar domestic mammals; probably the elephants; many of the ungulates, carnivores and rodents, especially those that live in warm and tropical regions.

Type No. 3.—Mating behavior of neither sex limited to short, definitely determined periods, but nearly always capable of manifesting itself, under favoring circumstances, in healthy adult and subadult individuals. Examples,—most of the primates that have been subjected to adequate study (several species of macaques; one species of baboon; several individuals of chimpanzee, a pair of orangs).

OBSERVATIONS ON THE FIRST TYPE

In *Type No. 1* the psychology of both sexes is, essentially, and so far as the species as a whole is concerned, subordinate to a definite, individual, mating rhythm, presumably determined by the presence of the stimulating hormones, in both sexes, during sharply defined, short periods only. The sexual behavior rhythms of female domestic mammals are well known. That the males of many kinds, among those not made familiar by domestication, follow an equally rigid periodic behavior pattern is not so generally realized. I shall therefore quote accounts of a few conspicuous examples of masculine subjection to rhythm.

Describing the rut of the whitetail deer, Seton (1909, vol. 1, pp. 104, 106) writes:

> As October comes on another change sets in with the bucks. Their necks begin to swell and their mating instincts to arouse. Hitherto they have been indifferent to the does when they met by chance, but now they set out to seek them. . . . . As November, the true rutting time, draws near, the necks of the bucks become enormously enlarged. . . . . Their whole nature seems to undergo a corresponding change at this time, and by November they are blind and mad with desire, as well as ready and eager to fight any of their own or other kind that seems likely to hinder their search for a mate.

The same author says of the moose at rutting time (1909, vol. 1, p. 169):

> The physiological change, called puberty in man, now sets in with the moose. He is subject, indeed, to an annual puberty. At other times he is exempt from the much-mingled pleasures of the fatuous epoch, and free to mind his own business. Early in September the rut sets in, with an exaggeration of everything that is male in his mental, moral, and physical make-up. He devotes all his energies to the matter in hand; he even neglects to eat; his all-dominant object now is to find a mate.

The sexual behavior of the male thirteen-striped ground squirrel is perhaps even more strictly governed by physiological rhythm than that of a male deer, for, while the buck when out of season is merely indifferent to the doe, Otis Wade (1927, p. 270) has observed that the male ground squirrel, after his short period of rut has passed, becomes positively antagonistic to the female. Of the animals that he had under observation Wade writes:

> Breeding activities are at their height during the last two weeks of April; however, this varies with the season. Some mating occurs earlier, and undoubtedly some well into May. One observation, which has an important bearing on this point, is that the males are sexually active for only about two to four weeks in the spring, more commonly for two than four weeks. This appears to be the chief factor governing the rutting season for I have observed females on a number of occasions willing to mate, both before and after the males were sexually active —though in more cases afterwards—and in a few instances for some time after the males had lost the rutting impulse. The following will serve as an example: On April 30, a male was put with an "old" female. They soon mated and the male was then segregated. The female did not become pregnant. As soon as the period of gestation [18 days] had

elapsed, she was put with five different males. In every case the female was willing to mate but none of the males was then sexually active and all refused to accept her, but instead were very belligerent and fought viciously when approached by the female in a friendly manner.

Of another North American rodent, the white-tailed prairie-dog, Alfred H. Stockard (1930, p. 473) finds that the males come out of hibernation early in March, to be followed by the females about two weeks later. Sexual activity then "continues within a time limit of two or three weeks for the entire population in a given locality. After this period a rapid decrease in size and content of the sex glands of the males occurs until they are approximately only one tenth of their previous weight." There is only this one breeding season each year.

Probably no example of a special, physiologically determined breeding psychology is more striking than the one presented by the males of the northern furseals (Elliott, 1884). During a great part of the year these seals lead a pelagic existence, their attention given over to the capture of fish. Sexual activities at sea are impossible, as mating can not take place in the water. In May and early June the males of the Alaskan furseal arrive at the Pribyloff Islands, where each individual takes up a position on the breeding grounds and fiercely defends it against his rivals, there to await the coming of the females. About the middle of June the females begin to appear. As they land they distribute themselves among the males, in the proportion of from two to fifty—usually from fifteen to twenty—females to each male. The entire energy of the breeding adult males during their stay on land, from early May until about the 10th of August, is given over to the sexual function in its two aspects of battling with other males and impregnating the females. The conflicts are most severe during the period when the bulls are establishing themselves on their stations before the arrival of the cows.

Throughout this breeding season of three months or more the digestive function of the males is wholly suspended, and sleep is almost eliminated. Elliott (1884, p. 84) thus pictures the complete absorption of the bulls in the business of sex.

> All the bulls, from the very first, that have been able to hold their positions, have not left them from the moment of their landing for a single instant, night or day; nor will they do so until the end of the rutting season, which subsides entirely between the 1st and 10th of August, beginning shortly after the coming of the cows in June. Of necessity, therefore, this causes them to fast, to abstain entirely from food of any kind, or water, for three months at least; and a few of them actually stay out four months, in total abstinence, before going back into the water for the first time after "hauling up" in May; they then return as so many bony shadows of what they were only a few months anteriorly; covered with wounds, abject and spiritless, they laboriously crawl back to the sea to renew a fresh lease of life. Such physical endurance is remarkable enough alone; but it is simply wonderful, when we come to associate this fasting with the unceasing activity, restlessness, and duty devolved upon the bulls as the heads of large families. They do not stagnate like hibernating bears in caves; there is not one torpid breath drawn by them in the whole period of their fast; it is evidently sustained and accomplished by the self-absorption of their own fat, with which they are so liberally supplied when they first come out from the sea and take up their positions on the breeding-grounds, and which gradually disappears, until nothing but the staring hide, protruding tendons and bones mark the limit of their abstinence.

A less highly specialized form of breeding association, based on the same underlying psychology, has recently been described by L. Harrison Matthews as occurring in the elephant seal of South Georgia (1929, pp. 239–240).

Two important circumstances in connection with type No. 1 are, first, that this kind of behavior occurs chiefly in

mammals that are subjected to conspicuous seasonal changes in climate, and, second, that it is usually if not always confined to mammals in which the males have a seasonal rhythm of spermatogenesis. Though we are still ignorant of the exact conditions pertaining to spermatogenesis in the great majority of mammals, we know that in many kinds the production of sperm does not continue uniformly throughout the year. Robert Courrier (1927, p. 176) has summarized the facts in a passage that I translate as follows:

> Mammals are divisible into two groups according to their testicular activity. Some have a germinal substance that constantly produces spermatozoa; they have *continuous spermatogenesis*; among them are, for instance: man, guineapig, rabbit, house mouse, rat, dog, cat, boar, horse, etc. The germinal substance of the others is active at certain times only, it is subject to seasonal variations; among these mammals with *periodical spermatogenesis* we find especially such wild animals as the mole, the bats, the European hedgehog, the marmot, the polecat, the weasel, the beech marten, etc.

John R. Baker (1930) recently studied the seasonal variations in the spermatogenesis of British mice of the genera *Apodemus* and *Evotomys*. In *Apodemus* he found that the testis may shrink from a maximum summer weight of over 900 milligrams to a minimum winter weight of less than 50 mg. "There was complete histological dedifferentiation in the minute testes of the winter of 1925–1926. No spermatocytes, spermatids or sperms are found in the tubules. . . . . The vesiculae seminales underwent a series of size-changes corresponding with those of the testes, varying from an average of about 10 milligrams in the winter of 1925–1926 to about 400 milligrams in the summers of 1926 and 1927." The corresponding data for *Evotomys* are not explicitly given. Similar observations on southern blue and fin whales have been published by Mackintosh and Wheeler (1929, pp. 405–412) and on the European common shrew by Middleton (1931).

It is also to be noticed that mammals belonging to families or genera whose usual behavior is of this definitely regulated kind may, either as individuals or as entire species, depart from the general rule, and display behavioral features that belong more properly to type No. 2 or even to type No. 3. Such a variation on the part of a species has been recorded by Blanford. Describing the habits of the axis deer (1888–1891, p. 549) he writes:

> "There is, I believe, much variation in the rutting-season. . . . . I am under the impression that young fawns are born almost throughout the year. Certainly there is great irregularity as to the period of dropping the horns, and bucks with perfect antlers may be found at all seasons."

Striking individual departures from the usual habits of a species have been observed in the American elk. This animal has an autumnal rutting season like all northern deer. During the rest of the year the sexes, as a whole, appear to be indifferent to each other. O. J. Murie, of the U. S. Biological Survey, who has given several years to a study of the elk herd in the Yellowstone National Park, writes me under date of April 16, 1930:

> I have never seen the slightest indication of sexual interest among animals on the winter range or on the feed grounds. I asked Mr. A. P. Nelson, who is in charge of the Elk Refuge, and he has seen no such actions during the years that he has been here. On the other hand I have frequently noticed that old bulls will "shoo" away younger bulls or cows equally from any choice bit of hay he might fancy and I know of at least three instances where a bull killed an adult cow, by puncturing the abdomen with a tine of the antlers.

However, a tame young bull elk kept at the government refuge showed no such limitation of his sexual impulse. In the letter from which I have just quoted Mr. Murie writes of this animal:

I caught him as a new born calf. He was raised on milk, and at the age of a month or so was given the freedom of the place. He is now almost two years old and wanders at will over the Refuge, but prefers to remain near the farm buildings and is perfectly tame and can be petted. Before this animal was seven months old Mr. Nelson saw him many times attempting to mount wild cow elk which wandered into the farm yard and it seems to be a regular habit with him. Last month, March 1930, I saw him mounting a domestic cow.

Seton (1925–1928, vol. 3, p. 43) records the case of a captive bull elk that successively established sexual relations with a mare and a gelding. Unfortunately he does not give any information as to the adolescent history of this animal. Of even greater interest is a note on the behavior of a bull elk published by Caton (1881, p. 315). It shows that the animal deliberately abandoned females of his own kind for one of a very different species, and also that the sexual potency of this bull continued throughout the period of antler growth. Caton writes:

When I had but one male elk, with several females, a strong attachment grew up between the buck and a two-year old Durham heifer, so that he abandoned the society of the female elk, as the heifer did that of the cows in the same inclosure with which she had been reared, and they devoted themselves exclusively to each other. When they laid down in the shade to ruminate, they were always found close together, and when one got up to feed, the other would immediately follow. They kept away by themselves, always avoiding the society of all the other animals. Whenever the heifer was in season, which occurred quite regularly every month, she accepted the embraces of the elk, without showing an inclination to seek the other cattle; nor did this seem to be the result of any constraint. This intercourse continued throughout the summer, during the entire growth of the antlers of the elk, but unfortunately he was killed before the rut commenced with the female elk.

The American pronghorn, whose sexual behavior, as a species, appears to be strictly of this type No. 1, is also known to show individual peculiarities. Caton (1881, pp. 45–46) quotes Canfield's account of a young animal in captivity. "When three months old, he commenced to leap upon other pet antelopes, the dogs, young calves, sheep, goats, and even people. . . . . He would in this way go at anything held up to him."

OBSERVATIONS ON THE SECOND TYPE

In *Type No. 2* the psychology of the female varies synchronously with an obvious physiological rhythm of the reproductive organs, but that of the male appears to be constant, stimulated, presumably, by a hormone always present throughout the period of sexual maturity. In well marked examples of this type, such as those so widely known in domestic dogs, cattle, sheep, goats, and swine, and as Warner (1927) has carefully studied in the white rat, the female is habitually sexless in her behavior except when she is in heat and not pregnant, but the male is responsive at any time to a female in appropriate condition. Rare instances of sexual behavior during pregnancy have been recorded in the rat by Long and Evans (1922, p. 58) and Nelson (1929); in the house mouse by Crew and Miskaia (1930) and Watt (1931).

A variant of type No. 2 has been described by Stockard and Papanicolaou and by Louttit as occurring in guineapigs. Louttit (1927) found the sexual impulse of the male to be so constantly active that the condition of the female had no specific influence in arousing it. Regardless of their physiological state the females were always sexually attractive to the males; nevertheless the females would not permit intercourse when they were pregnant or when they were not in heat. The males appeared to have no means of knowing when a female was in heat except by trial; and they would lose such a female in a group of others.

Stockard and Papanicolaou (1919, p. 229) say that "a male after long isolation from females becomes sexually excited by the presence of any female irrespective of her sexual condition, and he invariably attempts to copulate." The behavior of this animal would therefore seem to be intermediate between types 2 and 3.

As to its geographical distribution, type No. 2 appears to occur most commonly in warm or tropical countries where seasonal contrasts in climate have much less influence on the general living conditions of animals than is the case in northern regions. Slade (1903) believed this type to be present in the Indian elephant; Roosevelt (1910, p. 110; 1914, vol. 1, p. 382, vol. 2, pp. 585, 604) observed it in the topi, hartebeests, and gazelles of British East Africa; and Schuster (1929, pp. 115–116) has more recently recorded it in the reedbuck, hartebeest and gnu.

OBSERVATIONS ON THE THIRD TYPE

In *Type No. 3* the sexual psychology of the female as well as that of the male has been liberated from strict periodical oestrous control; or, what amounts to the same thing so far as behavior is concerned, the physiological stimuli to mating, though they may be stronger in the female at some times than at others, appear to be rarely if ever completely absent in either sex at any part of the year. The behavior patterns are not necessarily uniform at all seasons; but conspicuously marked physiological rhythms are no longer the nearly exclusive regulating factors in the mating behavior of either sex. Mating behavior becomes established as part of the play activities of young individuals, and from this early period onward until senility makes it impossible, it may occur at any time, even during pregnancy, when not inhibited by some unfavorable factor such as fear, fatigue, hot weather, molt, injury or ill health. Throughout its course it tends, in both sexes, to assume more nearly the form of an ever-available amusement activity than that of a periodic blind submission to an inescapable racial force. Individual variations of sexual behavior appear to be more common than in types 1 and 2.

This type of sexual psychology has been recorded as occurring in Orangs, Chimpanzees and several Old World monkeys and baboons, all of them tropical or subtropical in distribution.

The literature in which the real sexual behavior of non-human primates has been described is neither very extensive nor does it cover a long period of time. In all, there appear to be only about a score of papers by some sixteen writers. The first appeared in 1914, the last in 1931.

When the details recorded by these observers are fitted together they make a composite picture of sexual behavior in the higher non-human primates that conspicuously differs from the pictures we have just looked at as illustrations of behavior of the first and second types. The main outlines of this new picture have been thus traced by Zuckerman (1930, p. 748):

> The matings of the lower mammal are confined to short periods circumscribed by the activity of the follicular hormone. The matings of the primate are diffused over the entire cycle, paralleling the continued action of the follicular hormone, but varying in frequency according to the varying degrees of activity of that hormone.

(*a*) *Macaques and baboons*

The most complete account of the macaques is the one given by Hamilton (1914). Its main features I have already (1928, pp. 278–279) summarized as follows:

> Doctor Hamilton based his observations on twenty subjects, eighteen macaques (*mulatta* and *irus*) and two "baboons" named "Grace" and "Sandy" (ac-

tually, I am convinced, after corresponding with Doctor Hamilton, a female Celebean black ape, *Cynopithecus niger*, and a very large male pig-tailed macaque, *Macaca nemestrina*). The animals were kept part of the time in cages and part of the time in a state of semi-freedom, at a laboratory situated "in the midst of a live oak woods in Montecito, California, about five miles from Santa Barbara." . . . . . The females were not subject to a psychological oestrous cycle, but were ready to accept the male at all times when not physically incapacitated (as by traumatism or recent parturition). The adult males were sexually attracted by any adolescent or adult female at any time; their sphere of sexual interest was not limited to female individuals of their own kind, but was so widely extended as to include females of other species, also weaker monkeys of the male sex, and animals of the most varied sort (snake, kitten, puppy, fox, human infant, man's hand); autoerotism occurred, but not frequently, the only observed instance being that of a male when temporarily kept in solitary confinement. Hemosexuality was most frequent in immature males, least frequent in females. The absence of specific and single release of the sexual impulse was almost as evident in the females as in the males. Among them homosexuality was not absent, though it was far less frequent than in the males; one female went out of her way to establish sexual relations with a male dog, another offered herself to a ranch hand employed about the laboratory. Continuous confinement of one male with one female resulted in a marked diminution of sexual enthusiasm in both, particularly in the male; a condition that the animals sought to remedy by special stimulations often sadistic on the part of the male; vigor was immediately restored by supplying each with a new mate. Females and immature males deliberately employed sexual artifice either to bring enemies within reach of attack or to turn aside the aggressions of stronger animals. Sexual jealousy was well developed in both males and females.

Unlike the monkeys observed by Hamilton those studied by Kempf (1917) were kept under unnatural environmental conditions in cages. Of the six subjects all were *Macaca mulatta* (= "*rhesus*") and all but one were males. The female was immature and was less sexually attractive to the males than the individuals of their own sex. Hence the observations bear mostly on homosexuality. No period of heat was observed in the female; and nothing in the entire paper gives the slightest support to the idea that sexual response in a healthy male monkey is ever in abeyance. One male is described as conspicuously algolagnic.

Objections are frequently brought against research based on animals kept under unnatural conditions, but these objections mostly arise from the confusing of two different things, namely, the study of psychological reaction patterns and the study of the behavior of a species in nature. Laboratory surroundings provide unfamiliar stimuli and give inadequate information about activities in the wild; but it has yet to be shown that these stimuli are capable of doing anything else than to reveal the reaction patterns normal to the animal under investigation. The longest continued of all laboratory experiments, domestication, has not obliterated the essential psychological differences between horse and cow or between dog and cat. The unlike sexual traits of caged macaques and caged microtine rodents, which breed with equal freedom in captivity, cannot be attributed to unnatural surroundings, because these surroundings for both animals are alike.

Hartman's observations on *Macaca mulatta* (= "*rhesus*") are in accord with those of Hamilton. In his first paper (1928, p. 185) he writes: "as a rule the females will accept the male whenever given the opportunity . . . . the stage of the menstrual cycle has nothing to do with their refusal or acceptance." In his second paper (1931, pp. 136, 138–139) he gives a particularly interesting account of the depressive influence that adverse climatic and physiologic factors exercise on sexual behavior:

In the first place, the heat of summer is unfavorable to the monkey, at least to the tropical monkey. This is well known to animal importers and hunters. We find it so in the Carnegie Colony. By far the greater

number of deaths have occurred in the summer and fall months even among the "acclimated" individuals, though the death rate has been cut down since we have ameliorated the heat conditions by using a fine spray of water or "artificial mist" in the paddocks. The animals are more likely to lose weight in the summer, and they then shed their hair, which further exaggerates their unprepossessing appearance at this time. Menstruation is more irregular in summer, often absent entirely; moreover the sexes are far less interested in each other and the usually quite willing males may occasionally even entirely refuse to copulate. . . . . The low ebb of sexual activity in the Carnegie Colony in the summer months is therefore incontrovertible and the sterility of the animals is due to the absence of an ovulatory cycle, although menstruation continues. That the males are not sterile is shown by the repeated recovery of motile sperms from mated females and by a single conception on July 24 in a favorable female. Yet the males are less ardent in summer than in winter and refuse mating with some females altogether.

In his account of the self-mutilation of a male *Macaca mulatta* (= "*rhesus*") Tinklepaugh (1928) describes a case of monogamous attachment on the part of a young monkey, "Cupid," to the older female, "Psyche," (of another species, *M. irus* = "*cynomolgus*") that had sexually initiated him. So strong was this attachment that "Cupid" behaved with the utmost unfriendliness toward other females (of his own kind) with which he was brought in contact. It was only after a long course of "conditioning" that he could be made to accept them sexually; and, to all appearances, this treatment resulted in disturbing his mental balance to such a degree that finally, on being led between the cages containing the different females, he mutilated himself by inflicting, with his long canine teeth, no less than twenty severe lacerations on his legs, genitals and tail.

The baboons studied by Gear (1926) were five females and a male, all identified as *Papio porcarius*. The author writes:

During the dioestrus and metoestrus periods the behaviour of the baboons shows all the liveliness and vigour characteristic of the primates. They are continually on the alert, showing a restless interest in their toilet, their food, and their environment. Though the baboons were always on friendly terms with each other, yet, at dioestrus and metoestrus, the females would not tolerate any sexual advances of the male. During the period of the genital enlargement, however, a marked change in behaviour occurs. . . . . In the females under observation, it was at this time that they permitted and even solicited the advances of the male, resulting in frequent acts of coitus." His conclusion is that the [female] baboon shows a typical phase of desire occurring during the engorgement of the external genitalia.

These observations are partly confirmed by Zuckerman, who, however, found that the female hamadryas baboon will accept the male at other times than those of genital enlargement. Writing of the animals in the London Zoological Gardens he says (1930, pp. 729–730):

On "Monkey Hill," where a colony of hamadryas baboons of both sexes and all ages lives, it is possible to observe the behavior manifestations of the sexual skin cycle under relatively "natural" conditions. The bond between a male and his female is closest when there is greatest pudendal swelling. . . . . Copulation is most frequent during the stage of perineal enlargement, though it also occurs during the quiescent phase. When more than one female is owned by a male, priority in the harem is taken by the female "in oestrus." Under such circumstances the male overlord copulates almost entirely with the female who is in the phase of pudendal enlargement. I have never observed the male mating at such a time with a second female of the harem who is in the quiescent phase. . . . . The instances of "infidelity" which I have noted have involved only the quiescent female, never the "oestrous" female.

In an earlier paper (1929, pp. 86–87) he gave the following more detailed account of the social system that prevails among the hamadryas baboons:

The more or less recent establishment of colonies of Hamadryas baboons in many European Zoological Gardens has provided excellent opportunity for careful study of the social relationships of these monkeys under conditions approaching their natural environment as closely as is possible in a state of captivity.

These relations are in no way subjected to human interference. Observations made in London and Munich have shown that the internal arrangements of such colonies are always the same. Their more prominent features, without entering into detail, are as follows.

Each colony consists of harems, bachelors, and children. The individual harems never come into close contact with each other, and certain of them are more inclined to keep away from the main body than others. The "married" males in all cases dominate the "bachelors" who will invariably move away from any favourable spot in which they may be, on the approach of a harem.

Females are completely dominated by their males, following them wherever they go. The bond between male and female is, however, closest when the latter is "in oestrus." At such time the female hardly ever moves from the male's side, whereas in the quiescent phase she may sit several feet away from him. When more than one female is owned by a male, priority in the harem is taken by the female "in oestrus."

In some instances a male will follow readily where his female leads; in others, if a female wishes to move, or to remain where she is, against the male's desire, she attempts to get her way through sexual approach. Both sexes of all ages appear to present themselves sexually to those of their fellows whom they fear; this appears to be a means of diverting assaults.

All baboons manifest homosexual tendencies. Amongst males this type of response is most frequent amongst the "bachelors," though married males occasionally have homosexual relations, generally with "bachelors," and very rarely with each other. There is less homosexuality amongst females, and what there is is restricted to the members of the same harem.

Writing on the breeding season of non-human primates Zuckerman concludes (1931, p. 339) that such records as he has been able to tabulate "indicate clearly that monkeys can conceive at any time in captivity, and presumably, therefore, like the baboon, at any time in the wild." His field observations "prove conclusively that the chacma baboon of the Eastern Province of South Africa has no demarcated breeding season in its wild state" (p. 341).

(*b*) *Great Apes*

Turning next to the recent accounts of the great apes we find that no less variety of sexual behavior has been recorded, and that the studies, especially those of chimpanzees and of the gorilla "Congo," have been made with particular care and in great detail.

Montané (1915, 1928) appears to have been the first to observe a female chimpanzee that was ready to respond to the sexual advances of the male "frequently" and "at any moment," throughout pregnancy as well as at other times. Sokolowsky (1923) remarks that a large adult male chimpanzee confined in a cage with several females and a young male practiced "repeated intercourse every day with his females," and that when a female was unwilling the male would use bullying methods to obtain her consent. Köhler (1925, pp. 313–315), although he admits that he was not "able to obtain any adequate notion of the sexual behavior of chimpanzees," made, nevertheless, some very important observations, among them the following:

It seems to me that among these creatures sexual excitement is less specific, and less differentiated from any other kind of excitement, than among human beings. We may almost say that any strong emotion, and thus also any strong external stimulus tends to react directly upon both the colon and the genitals, but not so as to give the impression of exaggerated and concentrated sexuality, but rather of an extreme vehemence and interdependence of all vivid inner processes. We may even say that this extreme frequency of sexual effects implies a certain trivialization of this sphere of life, rather than its intensity. . . . . The female of the species definitely menstruates, at intervals of thirty to thirty-one days, and always for a period of between three and six days. During the flow her sexual instinct is absolutely quiescent, but her temper is often particularly amiable. After the cessation of the flow, there is an access of sexual desire, accompanied by a pronounced swelling of the whole external genitalia. At this time the animals

are irritable and uncertain in temper, and suffer a good deal from the very sensitive swollen area, until it subsides.

Passemard (1927) records the algolagnic attack of a male on a female, sexual interest on the part of this same old male in an unripe female, and the seemingly definite stimulation of another male by the sight of a particular woman. Fox (1929, p. 50) made observations on a pair of adult chimpanzees in Philadelphia that rather nearly coincide with those of Köhler. He writes:

Although the act was practiced frequently, day and night, during the interval between the heat periods, it was more prolonged and apparently more interesting to both animals, the female especially, during these periods. 'Heat period' means the duration of the perineal swelling [of the female]. The greater the swelling the more frequent the sexual act.

That the sexual behavior of the orang is equally free from oestrous limitation there can be little doubt. Fox says of the adult male and female in Philadelphia: "The act is practiced daily, without relation to the sexual cycle" (1929, p. 41). His account of the position assumed by the pairing animals is especially important because it appears to be the first record of female passivity during copulation in any nonhuman primate. Fox writes (1929, p. 41):

The copulatory act of our orangs is worthy of description because of its dissimilarity from that described for the chimpanzee. When the desire animates the male and is reciprocated by the female, he pushes and mauls her a little, whereupon she lies upon her back on the floor. The male then approaches her and separates her legs. During the act he remains in a sitting or crouching attitude and though they are face to face, he does not lie upon the abdomen of the female. The male will sometimes grasp a leg of the female and hold it up and to the side during the conjugation. During the act, there is no fondling, nor do they mouth each other either before or after the act. The female lies passive and often has a hand over her face.

In this connection the observations of Basedown (1927, pp. 151–154) on Australians, and Malinowski (1929, pp. 336–337) on Trobriand Islanders are of interest. Possibly the habit recorded by Fox is exceptional, as Paul Eipper (1929, p. 78) and Zedtwitz (1930, p. 285) have described postures in which both orangs were suspended by their hands from the bars at the top of the cage. G. Brandes (1930), however, gives observations on two pairs whose behavior almost exactly coincided with that recorded by Fox. One of the males is described as pulling his female about on the floor exactly as a man would handle a sack of potatoes. This does not necessarily indicate that the female orang is at the mercy of the male, as Zedtwitz (1931, p. 14) mentions an unsuccessful attempt by a male to "force" his mate.

As regards the gorilla we still lack observations on adult animals and on males. Yerkes (1927, pp. 520–522) has described the beginnings of sexual behavior in the young female "Congo." At an age believed to be about six years she began sex play with two dogs, a male and a female. The gorilla assumed the active part in this play, and the dogs were always either indifferent to it or annoyed by it. A year later she behaved in a similar and even more unmistakable manner toward men. "Her insistence on sexual contact," Yerkes writes (1928, p. 69), "was extremely embarrassing to us and somewhat dangerous because of her enormous strength, but throughout the period of observation she was unusually gentle and friendly, although determined in her efforts to satisfy her desire."

The gradual development of specifically sexual behavior out of the generalized activities of four young chimpanzees (two males and two females) has been carefully studied by Bingham (1928). Some of the more important of his observations are as follows:

The behavior of these young chimpanzees prior to December 10, 1925, included varieties of social adjustment having, to all appearances, no immediate sexual significance. In these adjustments, however, there appeared components of behavior which differ little, if at all, when appropriately united, from essential adjustments involved in copulatory relations. What appeared to be a new synthesis of responses was observed for the first time on December 10 and recognized as copulatory play. It seemed to involve no new elements in behavior although the adjustment as a whole was novel. Existing factors, previously expressed and developed as parts of other syntheses of responses, appeared to undergo reorganization while I looked on and witnessed initial adjustments of a copulatory nature (p. 78). . . . . These young animals merely repeated over and over the copulatory adjustments without copulation. The relations, it seems to me, may quite properly be termed copulatory play (p. 97) . . . . Repeated observations involving both males have convinced me that sexual manifestations are asserted in situations which elicit various kinds of excitement, including both agreeable and disagreeable experiences (p. 92). . . . . This copulatory play, years before reproductive maturity, is the most surprising behavior I have ever observed! There was remarkable cooperation between the pair. The functional adequacy of their behavior is astounding. . . . .I never expected to see such preadolescent behavior. Moreover, I am surprised at the front to front position. So far as I know, the lying, ventroventral position in the anthropoids has never been reported (p. 85). . . . . Presently they took the standing position of quadrupeds (p. 86). . . . . Following the initiation of mutual sex play, there were many repetitions and variations. Conspicuous differences appeared in ventroventral and dorsoventral adjustments. Other variations of significance were noticeable in the social situations that fostered copulatory play. Moreover, the variability that occurred in the sexual behavior itself appeared to be only a continuation of that which prevailed in the sources of such behavior. A heterogeneous group of variable activities, including both primitive responses and recent acquisitions, seemed to contribute in varying degrees to these sexual foci. Excitement—revealed by romping, teasing, petting, fleeing, eating, fighting, tantrums, and commonly by mixtures of these and other activities—was a consistent forerunner of sexual responses (pp. 155–156).

Bingham describes instances of exhibitionism of both types, namely, presentation of the sexual parts to visitors (pp. 131–135) and copulation incited by the approach of a visitor (pp. 14–17). The former was observed in chimpanzees of both sexes, and in a female gibbon; the latter was noticed in a pair of baboons and a pair of Celebean black apes. I have seen it in a pair of Barbary apes at the National Zoological Park, Washington.

In chimpanzees of both sexes he found masturbatory behavior well developed (pp. 139–151) and involving many different objects, such as hands (both sexes), toes (males), packing boxes (both sexes), measuring plane (male), a kiddy kar (male), mango fruit (female), leaves, small sticks and pebbles (female), pool ball (female) and combination of leaf and bars of cage (female). Passemard (1927) records it in the male chimpanzee that he believed to be sexually stimulated by the sight of a blond servant girl. My observation of the adult male chimpanzee in the National Zoological Park leads me to believe that, when thus engaged, he is indifferent to the visitors of both sexes near his cage. I have, however, repeatedly seen behavior of this kind directed toward adult visitors by a male drill and toward small children by a male Celebean macaque (*Magus maurus*), though in neither case with any apparent regard to sex.

(c) *American Monkeys*

In contrast to these rather full accounts of the sexual activities of Old World primates we find that very little has yet been recorded about the American monkeys. The only carefully made study that I have seen is the one pertaining to the common marmosets kept in captivity by Lucas, Hume, and Smith. About these animals the authors write as follows (1927, pp. 449–450):

On March 23rd [1926] coitus was observed, and also on the next two or three days. Then attempts became fewer and less acceptable to the female, and finally ceased altogether. During the ensuing months

there were no signs of oestrum, and when the young male was at liberty he paid no more attention to the female, through the bars of the cage, than he did to the other male. . . . . The night of August 19–20 twins were born. . . . . Pairing had again been observed on September 16th, 1926, and on February 4th, 1927, another pair of twins was born. . . . .

Miss Hume added, in a note published by Zuckerman (1930, p. 736), "that the time that elapses after parturition before a female will pair is variable. It has been observed after 23, 34, and 45 days. After a miscarriage only 12 days elapsed."

So far as these records are concerned it appears that the mating behavior of the common marmoset differs widely from that of the Old World primates whose habits have been carefully studied, and follows the pattern of type No. 2. It will be interesting to learn whether or not this type of behavior is widely prevalent among American monkeys, and also whether or not it occurs among the lemurs, about whose breeding activities I have been unable to obtain any information.

THE CLASSIFICATION OF HUMAN SEXUAL BEHAVIOR

It is obvious that human sexual behavior has little in common with behavior of the kinds that I have grouped under types 1 and 2. Among the animals that normally conform with these types, some individuals occasionally depart from the usual way of the species in a manner that parallels certain varieties of human activity; but among men and women we look in vain for tribes or individuals that normally or abnormally comport themselves, in affairs of sex, after the manner of deer and furseal or of cattle and dogs. That is to say, we do not find groups of people or even unusual persons of either sex whose sexual impulse lies essentially dormant throughout most of the year to awaken only during a short, seasonally determined, and excessively violent period of rut, or whose sexual activities, if not thus seasonally limited, are, nevertheless, restricted to short periods determined by recurrent physiological cycles in one or the other sex. The facts that have been recorded concerning seasonal periodicity in the sexual behavior of man seem chiefly to concern instances of recurring erotic festivals and slight but recognizable fluctuations in the birth rate (see Heape, 1900, pp. 34–38; Ellis in Moll, 1912, pp. 185–186). Tardieu, however, found a rather striking seasonal variation in the frequency of sexual assault in France, where, through a period of twelve years there were 4194 recorded cases during the months of May, June and July, as contrasted with only 2007 during November, December and January (1878, p. 23). But these human phenomena, like the falling off of sexual activity in macaques under the depressive influence of molt and hot summer weather (Hartman, 1931) appear to be reflections of seasonal changes in climate or in food supply or in other conditions that affect the general state of vital energy rather than strict behavioral reflections of physiological rhythms. On the other hand, when the sexual behavior of mankind is compared with that of nonhuman members of the order Primates, the natural group of mammals to which man pertains, the discrepancies vanish. To realize this the reader has merely to peruse the foregoing summary of laboratory findings and mentally translate the details into terms of human activities in the field of sex.

Perhaps the psychological rhythms noted by Gear (1926) and Zuckerman (1930) in baboons and by Köhler (1925) and Fox (1929) in chimpanzees, as well as the female aggressiveness described by Tinklepaugh (1928) in a macaque and by Yerkes (1928) in a gorilla may at first

appear unusual when viewed from the accustomed human standpoint. But when these observations are considered in connection with what is known of psychological rhythm in women (see, for instance, Davis, 1926; Ellis, 1928, pp. 213–236; Hamilton, 1929, pp. 196–197) they lose their strangeness; and when the macaque "Psyche" and the gorilla "Congo" are placed side by side with Retif de la Bretonne's Marie and Nannette (1883, vol. 1, pp. 52, 106–107) or Rousseau's Madame de Warens (1914, vol. 1, pp. 313–319) the action of these animals at once becomes humanly comprehensible. Tardieu (1878, pp. 65–71) and Ellis (1904, pp. 173–179) have, moreover, fully recognized the aggressive phase of human female behavior; Hamilton (1929, p. 349) has reported that in the cases of 14 among the 100 men whose histories he studied it was the women who took the initiative in the first sexual experience. Furthermore, it is to be remembered that the physiological rhythms of the female primates under discussion do not set the sharp limits on sexual behavior that we see in mammals of types 1 and 2. Even Zuckerman, who lays much stress on the importance of these rhythms, recognizes that their influence on behavior is only partial. He writes (1930, p. 749): "Monkeys that copulate in captivity do so at all times, but copulation occurs most frequently during the period of maximum sexual skin activity."

More important, perhaps, than any single one of these points of agreement is the fact that although the sexual activities of nonhuman primates have been carefully studied during less than two decades and in a relatively small number of species, they furnish a picture that almost covers the entire field of sexual behavior in man. This generalized-primate picture contains all of the "normal" elements of human behavior that are supposed, both popularly and by many technical writers, to distinguish man from other mammals. It also contains the more conspicuous of the elements that, because they run counter to social conventions, are usually designated as "abnormal" or "contrary to nature." Finally and very significantly, it includes few if any important features that lack some counterpart in the behavior of man.

We are therefore forced to conclude that human sexual behavior is not something isolated and unique. It is merely a common type of primate sexual behavior with a few specialized characteristics, exactly as the human body is a primate body specialized along particular lines. Attempts to understand it without taking into account the psychology of all primates must therefore be as futile as attempts to understand human anatomy without dissecting any other creature than man.

THE SPECIALIZED ELEMENTS IN HUMAN SEXUAL BEHAVIOR

Having now seen something of the points of agreement between human sexual behavior and the corresponding behavior of several non-human primates we may turn to the points of difference. Immediately we are struck by a significant circumstance. Whereas the points of agreement pertain, almost without exception, to elements of fundamental biological importance, most of the points of difference are of a nature that makes their existence, or at least their exact form, depend chiefly on human culture.

Such human behavior patterns as the various forms of clothing fetishism probably have no real homologies in the behavior of non-human primates, and the same is probably true of fetishism with regard to parts of the body; all appear to be dependent on the human habits of wearing clothes and of artificially modifying

sundry physical traits. Nevertheless the distinctly sex-tinged emotional attitude of monkeys toward the process of cleaning each other's fur and skin has been noticed by Zuckerman (1929, p. 78), while Tinklepaugh (1931, p. 430) has recorded a case of persistent modification of a female macaque's facial appearance by hair plucking done by her mate. From such beginnings the human "aberration" might arise. Even more strictly cultural in its nature is eonism or transvestism, where the unusual behavior is associated with a highly specialized convention in dress. Narcissism and pyrolagnia are other human peculiarities that seem to owe their being to conditions built up by man himself. The same is true of necrolagnia and psycholagnia. Certainly nothing could appear more unlikely than the origin of pyrolagnia and narcissism among creatures not provided with fire and mirrors; while the development of necrolagnia, undinism and coprolagnia among animals whose mental attitude toward death and the excretory functions is no more complicated than it is in the monkeys and great apes seems almost equally improbable. Bingham, however, (1928, p. 140) reports that he has observed erection reflexes in female chimpanzees after urination and defecation, and Hamilton (1928, p. 304–305) has described rudimentary anal eroticism in monkeys; while Köhler (1925, pp. 83–84, 309–310) gives an account of emotional elements in the reactions of chimpanzees to their own excrement.

Another specialized human mode of behavior has been described under the name of kleptolagny (Kiernan, 1917; Ellis, 1928, pp. 477–491). In its fully developed form this behavior would certainly depend on the human high regard for personal property, the violating of which would furnish the emotional stimulus that in rare individual cases might overflow into the sexual sphere. Nothing of exactly this kind has been recorded of any non-human primate; but a personal observation seems to furnish a definite analogy. A half grown baboon (*Papio cynocephalus*) in the National Zoological Park succeeded (February 20, 1930), after long effort, in removing the baseboard from the front of his cage and dropping it on the floor. As soon as the keeper came to replace the board the baboon resisted strenuously, pushing the board away with hands and feet. At the same time he developed a full erection that did not subside until the board was securely fastened back in place and another keeper had arrived with food. In this animal, as in the kleptolagnic shop lifter, mischief and sex went hand in hand.

Masochism deliberately resorted to as a means of sexual gratification is not mentioned in any of the accounts of non-human primates that I have seen. Nor have I noticed any suggestion of it among the primates in the National Zoological Park. Doctor Bingham's remark (1928, p. 92) that sexual manifestations are sometimes asserted in situations that include disagreeable experiences seems, however, to point to its germ.

Psychological hermaphroditism appears to be equally common in man and in all the non-human primates that have been adequately studied. It is known to occur in other mammals; but there is little doubt that it reaches its highest development among the primates, and that when he indulges in this type of behavior, man is merely acting in accordance with one of the normal rules of his order. Complete homosexuality is, however, so far as can now be judged, a special human exaggeration of this widely prevalent primate tendency. On this subject Bloch (1908, p. 530) expressed the extreme opinion that

> Original, congenital, enduring homosexuality would appear to be an exclusively human peculiarity. It is very doubtful whether a similar condition exists among animals. We recognize among the lower animals homosexual acts, but no homosexuality. Thus we have no phylogenetic starting-point for the explanation of homosexuality.

More recently William J. Robinson has written (1929, p. 383):

> Moreover, this particular perversion is not found strictly speaking among the lower animals, as is the case with most other perversions of the sexual instinct. Of course, homosexual acts have been observed in the life of various animals, but these have been isolated instances, nothing habitual, nothing to justify the conclusion that homosexuality or inversion is an established custom among them. P. Naecke has studied pederasty in animals. The literature on pederasty and tribadism among animals has been analyzed by Karch. The observations of these writers strengthen the conclusion that such perversions are incidental occurrences among animals and that true inversion, as a more or less permanent state, such as is found in man, is peculiar to the human race only.

It is obviously an exaggeration to deny any phylogenetic starting point for the extreme condition met with in man, because there is strong evidence in favor of the view that adult human homosexuality often results from the fixation, by cultural influences, of behavior patterns that are common to young primates of several kinds, man included, and that would tend, under natural conditions, to be superseded by heterosexual behavior after puberty (see especially Hamilton, 1925, pp. 153, 301, 306–307). Nevertheless there is no doubt that permanent adult homosexuality in other mammals is excessively rare, though a case somewhat approaching this condition in a bull is recorded by Seton (1927, vol. 3, p. 43). The only behavior even remotely suggesting it that I have seen in a non-human primate is that displayed by two female sooty mangabeys (*Cercocebus fuliginosus*) now living (1931) in the National Zoological Park. These animals have been confined together for about ten years. When received they were nearly full-grown. They frequently indulge in homosexual play. On the sole occasion when a male was placed in their cage they took no sexual interest in him but attacked him so viciously that for his safety he had to be removed. Quite probably, however, this was merely a case of resentment against an intruder in the home.

The foregoing types of special human behavior are, it will be easily seen, of no very great biological or social significance. We finally come to two that are more important.

The first of these is that in man there appears to be a stronger tendency than in other primates for the members of a pair to become "conditioned" to each other in such a manner as to lead to long association of an exclusive or mostly exclusive kind. This tendency, which seems to form the basis of the complex sentiment defined by McDougall (1923, p. 425 and 1926, pp. 162, 560) as "tender passion" or "sex love," is known to be highly developed in a few birds, of which the domestic pigeon is a familiar example. Among mammals, however, it cannot be regarded as definitely proved to be common, because many of the supposed cases of natural monogamy rest on such anecdotal, uncritical evidence that they can not be accepted as free from a large element of doubt. Even the best attested instances, like some of those reported in carnivores, may depend on sparseness of population rather than on habit or instinct. Certainly, among mammals there is no known example of a monogamous species comparable with that which we see in the domestic pigeon. And it may be declared with equal confidence that no other primate has yet been shown by properly con-

ducted observations to form, habitually, such lasting attachments between sexual partners as those that are not uncommon in man. As to the behavior of wild primates we have, to guide our opinions, nothing more than field records of pairs or family groups seen together on particular occasions; we know nothing of the duration of such groups. In favor of the view that some non-human primates form at least temporary sexual alliances we have, however, Kempf's (1917), Bingham's (1928) and Zuckerman's (1929 and 1930) significant records of individual dominance and favoritism, and Tinklepaugh's (1928) observation of the strong attachment of a young male macaque to an older female.

The second socially important peculiar feature of human sexual behavior is that man alone of all primates, and probably of all mammals, possesses both the psychological and physical specializations needed to establish the recognized and always present possibility of rape. Even granting that rape may take place, on rare occasions, in other mammals, its essentially human character seems to be beyond serious doubt. Rape may be regarded as a by-product of human ingenuity seconded by the upright human posture with its specifically human remodeling of the primate pelvic region. This remodeling has brought the vaginal orifice into a position relative to the adjacent parts that renders sexual intercourse possible with a resisting or unconscious female forced to lie—or lying helpless—on her back. In quadrupedal and imperfectly bipedal mammals this orifice is so placed that the female voluntarily cooperates with the male in order to effect conjunction of the sexual organs. Except in man, aided by superior intelligence and favorable anatomy, unconsciousness or active resistance on the part of the female normally renders the sexual act impossible. The monkeys studied by Hamilton (1914) and Kempf (1917), as well as the chimpanzees observed by Montané (1915, 1928), Passemard (1927), Bingham (1928) and Fox (1929) presented no exception to this rule. The same was true of a pair of gibbons (*Hylobates leucogenys*) recently living in the National Zoological Park. During copulation both animals hung suspended by their hands from the bars at the top of the cage. The male approached the female from behind, and she, if in responsive mood, remained stationary and raised her knees, while the male curled his pelvis under hers but never grasped her in any way. The female then disengaged one hand (apparently always the left) and, passing her free arm back of the male's neck and body, voluntarily established the required intimate contact. If not responsive the female simply continued to "brachiate" and to pay no attention to the solicitations of the male. According to the keepers copulation continued uninterruptedly throughout a pregnancy that terminated December 27, 1930, in the birth of a healthy infant.

Attempts at sexual coercion on the part of non-human male primates have been recorded by several observers; but this procedure has not been seen to lead to the desired result unless it first induced the victim to cooperate. No instance of actual rape in the sense of copulation forced on a vigorously resisting female appears in any of the published accounts of laboratory observations. Nevertheless, the not infrequently observed attempts at forceful methods, added to the partial adjustments to the ventroventral posture in young chimpanzees as described by Bingham (1928), and the passive behavior of female orangs as recorded by Fox (1929) and Brandes (1930) appear to supply the rudimentary adjustments needed for leading up to the specifically human elimination of

female consent as a necessary part of the sexual act.

THE SOCIAL IMPLICATIONS

The great importance of comparative psychology in explaining the origin of some of the human behavior patterns that have influenced social development has been particularly emphasized by Kempf. His conclusions (1917, pp. 153–154) seem worthy of quotation almost in full.

In the infrahuman primates as well as in the genus Homo, homosexual interests predominate and normally precede heterosexual interests until the adult stage is well established. Homosexual interests occur in both sexes but are more common in the male.

The acquisition of an adequate sexual object for the affective cravings promptly proceeds if it is not inhibited by fear.

The transfer of the affective cravings from a homosexual type of object to a heterosexual object is a very delicate biological procedure and one that must not be inhibited by fear.

Reversion to homosexuality in isolated groups of males or females, such as prisoners, soldiers and sailors, normally occurs if adequate outlets for sublimation are not provided.

Submission as a homosexual object is implicated with biological inferiority in the infrahuman primate. This is probably the phylogenetic root of man's conscious, ineradicable recognition of homosexuality as a biological deficiency.

In the infrahuman primate as in man, sexual submission is practiced in order to procure food (clothing), and protection.

Catatonic adaptations are reflexly practiced by the infrahuman primates as well as by the human primate as a defense.

Vicious, diverting counter-attacks upon an inoffensive object are used for defensive purposes by monkeys. This is in principle comparable to the persistent, systematized counter-attack of the paranoid type of psychotic as a defense to avoid consciousness of his biological deficiencies which persecute him.

The infrahuman primate tends to adopt a variety of animals that do not cause fear, for his sexual cravings; a step preceding the permanent adoption of animals for his affective cravings by primitive man. This principle, of sexual substitution, was probably the foundation of that tremendously important step in man's biological career, namely the subjugation of herds, packs and flocks.

The phylogenetic constitution of man, as we find it completely exposed in the infrahuman primate, obsesses him with what he feels to be perverse tendencies as he strives to behave in an ideally civilized manner and plunges him into the depths of despair when he fails.

It should now be evident that the more conspicuous among those human forms of sexual behavior that are usually regarded as "abnormal" or "contrary to nature" are nothing more than little if at all modified aspects of traits so widely prevalent among primates that they must be recognized as parts of the racial heritage of every member of the order. This is particularly true of autosexuality, homosexuality, zoophilia, and active algolagnia, all of which have been frequently observed in laboratory animals. Bingham, as we have seen, has discovered in chimpanzees the tendencies that may easily represent the beginnings of passive algolagnia. In these directions man has done little more than specially cultivate a few elements of his primate patrimony, without producing anything essentially new; though a few somewhat unimportant human behavior patterns such as eonism, fetishism, kleptolagnia, narcissism, and pyrolagnia appear to stand rather specifically to his credit.

Any one of these socially condemned peculiarities may be of great and sometimes tragic importance to the man or woman that possesses it; but there is no reason to believe that all of them together have had much influence on cultural evolution. When, however, we turn to the admittedly "normal" elements of human sexual behavior we find at least four that seem likely to have taken very significant parts in determining the exact forms of many social institutions.

The *first* and most fundamental of these "normal" elements is the circumstance that human mating activities belong un-

equivocally to type No. 3. These activities, therefore, just as in most other primates whose sexual psychology is known, are practically always ready to manifest themselves, that is to say, they are never the abject slaves of seasonal and physiological rhythms that they are in mammals whose behavior follows the patterns made familiar by deer and dogs.

The *second* "normal" element is the human exaggeration of the tendency to form continuing associations between sexual partners. Hamilton, Kempf, Bingham, Tinklepaugh, and Zuckerman have described numerous imperfect examples of this tendency as displayed by monkeys and great apes. Its variability and capriciousness as we find it in man are well known; but it appears to be, nevertheless, sufficiently prevalent and well enough developed to have acted as an effective social force.

The *third* "normal" element is a trait that man and some other primates possess in sharp contrast with mammals whose sexual behavior conforms with type No. 1 or type No. 2, in both of which, on account of the shortness and violence of the sexual seasons, there is little if any possibility that it could ever become highly developed. (Lataste, however, 1886, p. 400, has recorded a trace of it in a male gerbil.) As a social force it is directly opposed to the permanent mating tendency. Kempf has described it so well that I shall again quote from him (1917, pp. 142–143).

> Sexual indifference may result . . . . from fatigue of the sexual sensorimotor system through excessive stimulation by a too constant object. . . . . Hamilton has . . . . reported that monkeys, when they are sexually semifatigued, expose their erotogenic receptors to intensive stimulation of an adequate nature before copulation recurs, and yet the same monkey in such a condition of sexual indifference to his companion, if allowed to have another mate, may rush into a sexual embrace with great excitement and without previous stimulation; apparently reacting to the new stimulation of his distance receptors. Similar behavior also occurs in man. . . . . Perhaps no other feature of the constitution of man has caused so much social turmoil and self-imposed distress as this phylogenetic predisposition of his affective-sensorimotor system. He likes to think of it as an impersonal thing and calls it the work of the devil, evil, immorality, the result of the sins of Adam and Eve, the wickedness of the flesh, and threatens his unruly neurones with the pains of hell fire and even castration. Hatred, anxiety, divorces, insanity, suicides, murders and social ruination commonly result from the conflicts with this phylogenetic predisposition of erotogenesis.

The *fourth* "normal" element is the human male's ability to force his female to accept a mating against her will or when she is unconscious. In every other mammal whose breeding habits have been properly studied the final act of mating depends on the consent of the female; without this consent and the cooperation that goes with it, the male cannot carry out his purpose, no matter if, as in the fur-seals, he may exceed his female six times in weight and incalculably in strength. Several carefully observed examples of female control of the sexual decision have been given in the course of this paper (pp. 384, 387, 389 and 395); others were described by Lataste, 1886–1889 (four species of gerbil, house mouse, Norway rat, guineapig); while additional instances have been more recently recorded by Heape, 1905 (rabbit), Svihla, 1930 (red-backed mouse), and 1931 (Texas rice rat), Svihla and Svihla, 1931 (muskrat), Stockard and Papanicolaou, 1919 (guineapig), Marshall, 1904 (ferret), and Wright, 1931 (skunk). Both sexes are fully aware of these conditions; their reciprocal behavior reflects this knowledge. It is not impossible that exceptions to the rule of female control may sometime be discovered among mammals other than man. But, if they occur at all, such exceptions seem likely to be so uncommon as to have little

or no influence on the formation of species habits. In man the conditions are radically different. Here the males possess the ability to take sexual advantage of their superior physical strength, and this circumstance appears to have made an indelible impression on the thinking and acting of the species as a whole.

The influence of these four "normal" elements of human behavior can be traced in the social systems of all peoples. This is inevitable because an important part of every such system is the experimental handling of a problem in which those elements play a very important part. Man is a gregarious, property recognizing primate whose sexual behavior is not subject to great seasonal or other fluctuation, whose young pass through an exaggerated phase of the long period of dependence on the parents common to most primates, whose adults possess the incompatible tendencies to form long continuing sexual partnerships and to become sexually indifferent or antagonistic through exclusive association, and, finally, whose males have the very unusual power to force their sexual will on the females. When he began to live in groups more intricate in structure and more dense in population than those that met the needs of other primates man found that these natural characteristics did not lead to harmonious sexual adjustment. They had to be checked and modified by cultural controls. How, then, should the required checks be applied? In their marriage customs the existing tribes and peoples have brought forward countless attempted solutions of this baffling and perhaps insolvable problem, as may be seen particularly well recorded in such works as Westermarck's *History of Human Marriage*, Margold's *Sex Freedom and Social Control*, and Briffault's *The Mothers*.

No one doubts that the conflict between man's strong inclination to form sexual partnerships and his primate tendency to tire of his mate is one of the disturbing elements in every social system. It has supplied the material for much of the world's literature and drama. Nothing further will be said about it here. But the cultural importance of the facts that human sexual behavior is in accord with mammalian type No. 3 and that in man alone among mammals the ability to make the final sexual decision has passed from the female to the male needs a few more words.

MAN'S SEXUAL BEHAVIOR TYPE AND THE PROBLEM OF PROMISCUITY

Among the many controversial details pertaining to our ideas about human social beginnings one of the most discussed is the question whether or not the existing forms of marriage have been developed from an earlier system or condition of sexual promiscuity. On this subject the most diverse and contradictory opinions are to be found in the writings of experienced authorities. For instance, Bloch declared (1908, p. 188) that

> Since the subject first engaged my close attention, it has always seemed to me incomprehensible that a dispute should ever have arisen among anthropologists, ethnologists, and historians of civilization as to whether, among the primitive forms of the sexual relationship, marriage was the first, or whether it was preceded by a state of sexual promiscuity. Whoever knows the nature of the sexual impulse, whoever has arrived at a clear understanding regarding the course of human evolution, and, finally, whoever has studied the conditions that even now prevail, alike among primitive peoples and among modern civilized races, in the matter of sexual relations, can have no doubt whatever that in the beginnings of human development a state of sexual promiscuity did actually prevail.

Westermarck, on the contrary, devotes no less than 234 pages of the revised edition of his *History of Human Marriage*

(1922) to a criticism of the hypothesis of promiscuity. His attitude may be learned from the following quotations (vol. 1, pp. 103, 336):

> It is often said that the human race must have originally lived in a state of [sexual] promiscuity. . . . . This opinion has been expressed by Bachofen, McLennan, Morgan, Lord Avebury, Giraud-Teulon, Lippert, Kohler, Post, Wilken, Kropotkin, Wilutzky, Bloch, and many others. . . . . It is not, of course, impossible that among some peoples the intercourse between the sexes may have been almost promiscuous. But the hypothesis according to which promiscuity has formed a general stage in the social history of mankind . . . . is in my opinion one of the most unscientific ever set forth within the whole domain of sociological speculation.

More recently Briffault (1927, vol. 2, pp. 1–96) has severely criticized Westermarck's handling of data. He concludes that marriage is an economic relation not originally associated with claims of exclusive sexual possession, and that freedom as regards extra-marital sexual relations is wide-spread and subject to little or no opprobrium in most societies. Economic considerations may in rare cases set a price on virginity; but the facts derived from a survey of all the cultures with which we are acquainted do not warrant the assumption that a regard for prenuptial chastity is widely held. Furthermore, he writes (1927, vol. 2, pp. 95, 96; 1931, p. 69):

> Individual marriage is, in its origin, not rooted in any form of association between sexual partners, or in any group, or family, resulting from such association, but is, even in its most primitive and rudimentary forms, distinguished as a juridic relation, irrespectively of its stability or of any group or family which may or may not be formed from sexual relations that are not thus juridically established. . . . . Very commonly, and in quite primitive societies, the juridic relation is not established until relatively late in life, on the ground of purely economic considerations; but sexual relations not so established, that is to say, pre-nuptial relations, are not in any way regarded as irregular or derogatory.
>
> Whether it be supposed that the earliest human social aggregates were formed by the multiplication and continued association of single pairs, or by the aggregation of several groups, comes to the same thing. According to every biological precedent the larger group must, in the absence of evidence to the contrary, be assumed to have been entirely promiscuous as regards sex relations. The problem of social origins is that of accounting for the introduction of sexual restrictions and regulations in such a promiscuous group.

After reviewing what is actually known of social grouping in non-human primates Zuckerman concludes (1929, pp. 83, 88):

> The harem is the social unit of monkeys and apes, and one may recognise two main types of society arising from it. The first, exemplified by the societies of the majority of tree monkeys, consists of the single harem living alone. The second is the society formed by the union of several harems. The best examples of this type are the societies of baboons, who are very seldom reported in troops of less than twenty, and have been seen in hordes consisting of as many as three hundred individuals. An intermediate type also occurs, several harems uniting to form temporary associations.
>
> It was from a similar social level, so far as one can tell, that, in the Oligocene or Miocene, an anthropoid set out on its journey towards manhood. Nothing is known about this journey. At the one extreme there is the anthropoid in its harem, a frugivorous animal who reveals just the beginnings of a reasoning process. At the other is man, whose every activity is culturally conditioned. The only possible social sphere of comparison between the two is the family, yet nowhere in the human world does one see anything approaching the harem of the infrahuman Primate. One fact is, however, clear. There is no need to search for cultural factors to account for man's permanent sexual association [i.e. permanent association in groups consisting of both males and females], for this feature is one shared by all Primates alike.

These opinions are representative of the many that have been expressed. Part of the conflict among them seems to arise from the circumstance that many writers not only human but also primate, and that leave out of account the fact that man is some lines of cultural development may therefore have had their beginnings among ancestral creatures that were not the same as the men of today. Lowie, for instance,

declares, in discussing the question of early promiscuity (1930): "Nevertheless, it holds true that *on the human level* (italics his) the individual family is never abrogated by such usages [sexual licence]. I, for one, am dealing with Andamanese, Australians, Chukchi, not with *Homo alalus*, or *Pithecanthropus*." To writers who thus limit their attention to conditions existing in living races the discovery that some trace of social control of the mutual relations of the sexes can everywhere be found today proves that man has always exercised such control. This conclusion, however, neglects the very important circumstance that no living race of man is primitive in the zoological sense. But the fact cannot be too strongly insisted upon that all present day races, whether considered as primates or as members of the family *Hominidae*, are highly specialized physically—for instance, in their gigantism and in the advanced adjustment of their skull, pelvis, and foot to the upright posture—and that this specialization points to the former existence of many long series of extinct races with which we are not now acquainted. Hence the search among these specialized existing peoples for a race or tribe living under social conditions that represent anything closely resembling an unmodified reflection of man's primitive mentality can have little chance of success. Another significant fact that has not been given its due weight in these discussions is the obvious circumstance that the principal checks imposed by every group on the sexual conduct of its members are checks on promiscuity, that is to say, checks imposed, for the benefit of some cultural scheme, on mammalian behavior of type No. 3.

A final source of confusion lies in the ambiguousness of the term *promiscuous* as it is commonly used. It is quite possible that few mammals are promiscuous in the extreme sense of breeding without any trace of individual choice on the part of either the male or the female. If this definition be insisted on the term necessarily becomes meaningless as applied to man and other primates. Nevertheless it appears to have been the one used by Zuckerman (1930, p. 725) when he wrote: "Moreover, monkeys are not promiscuous. The literature provides sufficient evidence to enable one to make the generalization that the tendency of sub-human male primates is toward polygyny. Every adult male attempts to secure for himself as many females as possible. There is no selection." On the other hand, promiscuity in the sense of the habitual formation of temporary, fluctuating, sexual associations is a term applicable to much of the recently observed primate behavior. This appears to be the usually accepted meaning of the word. It is the one that I here adopt.

It would be difficult to imagine a more convincing picture of a mammal fundamentally promiscuous, as the word has just been defined, than the one painted by Westermarck in the six chapters of his criticism of the hypothesis of human promiscuity. Only, instead of approaching his subject directly, after the manner of Kempf or Hamilton, he approaches it indirectly by outlining the multitudinous devices adopted by different social units in their attempts to modify a kind of behavior perfectly suited to the needs of primates roaming the forest in relatively small, simply constituted bands, so as to make it fit the needs of primates that have developed more sedentary, larger, and more complicated social groups.

EVIDENCE OF PROMISCUITY FURNISHED BY OUR OWN SOCIETY

Furthermore, when we examine the society that we know best, namely, our

own, we find abundant evidence that a considerable part of the sexual activity of its members is regulated even today by the rules of promiscuity that grow out of behavior type No. 3.

As long ago as 1904 Frey wrote (as quoted by Bloch, 1908, p. 190):

> Ports in which ocean-going vessels come to harbor are familiar with the sexual impulse in its most completely animal form. . . . . We find ourselves transported into the depths of an urgent primitiveness . . . . and this will enable us to form an idea of the bestia' indifference in sexual matters that must have obtain amongst the herds of primitive man.

But it is not necessary to visit sailor's resorts in order to obtain evidence that this "urgent primitiveness," or, in other words, behavior type No. 3, is constantly at work. The annals of prostitution illustrate it perfectly. Prostitution is often studied as a strictly economic phenomenon. And, undoubtedly, many women are driven to it by poverty. But the fact is generally overlooked that this form of activity could not offer the slightest relief from economic pressure to any mammal that might be psychologically monogamous, or to one whose sexual behavior was not of the type No. 3, that is to say, it would be economically valueless except to one whose female was always both attractive and receptive and whose male was always producing sperm. How true this is will be realized if we reflect on the economic worthlessness that prostitution would possess if the human breeding instinct were active, as it is in some mammals, during a single yearly period of a few weeks only; or if the sexual attractiveness of the human female to the male were limited, as it is in many other mammals, to a few days in each month. The conduct of the prostitute and her patrons seems, therefore, most reasonably interpreted if it is regarded, not as a social phenomenon generated by the forces of specialized civilizations, but as the commercialized survival of a promiscuous condition through which every human society has probably been forced to pass, by virtue of man's primate sexual behavior type.

While no adequate statistics can be found in print there is little cause to doubt that prostitution in European society and its derivatives, is both abundant and widely spread. Prostitution therefore cannot do otherwise than furnish to the many members of that society, both male and female, who desire it, for one reason or another, the opportunity to live a sexual life—temporarily or permanently—that conforms with a common primate type of behavior. The ease with which this mode of life is adopted has puzzled many moralists. It is not hard to understand when viewed by comparative psychology's light.

Another good indicator of the wide extent to which promiscuous behavior prevails in our society is furnished by the history, both past and present, of the venereal diseases. Buret has given (1895) an account of the epidemic of syphilis that swept through Europe at the end of the fifteenth century. The rapidity with which the disease spread is clear evidence of the sexual promiscuity that existed in the European society of four hundred years ago.

Coming down to the present day we find that there are differences of opinion as to the incidence of the venereal diseases in the general population.

Cabot (1916, pp. 365, 366) found that 33 per cent of the men over 16 years of age examined in the medical wards of the Massachusetts General Hospital (Boston) were aware that they had had gonorrhea. Syphilis was less prevalent in their recollections; nevertheless "about 25 per cent of hospital patients show a positive Wassermann reaction." During our partici-

pation in the world war Levin (1919) calculated, on the basis of more than 10,000 blood tests administered to newly enlisted soldiers gathered from all walks of life, that the proportion of syphilitics was about 16 per cent among the white men and about 36 per cent among the colored. Stanley (1929) has reported that 15 per cent of 10,000 male prisoners examined in the California State prison gave a history of venereal sore. The positive Wassermann reactions were as follows: white men (8,004), 7.2 per cent; negroes (530), 18.1 per cent; Mexicans (1,265), 15.6 per cent. Wassermann tests given to 1976 patients (sex not stated) in the Moses Taylor Hospital, Scranton, Pa., showed a positive percentage of only 6.3, as communicated to me by Dr. J. M. Wainwright. Concerning gonorrhea, Dr. J. Allen Gilbert, assistant professor of medicine in the University of Oregon, and medical adviser, Oregon Board of Health, declares (1916, p. 53) that we are perfectly safe in saying that from 70 to 75 per cent of all adult men have had the disease at some time in their life. Among the California prisoners Stanley (1929) found that 48.2 per cent "gave a history of gonorrhea which cannot well be mistaken." Blashko and Erb (as quoted by Bloch, 1908, p. 394) independently found, in Germany, that of the men who entered on marriage for the first time when above the age of thirty years, each one had, on the average, had gonorrhea twice, and about one in four or five had been infected with syphilis. Whichever figures or estimates are taken as most nearly representing the truth it cannot be doubted that they give unmistakable evidence of wide spread behavior in perfect conformity with type No. 3.

There is thus abundant proof that the tendency to behave promiscuously exists in our own society; and the same is true of every society with which we are acquainted. It is equally clear that all marriage systems are largely devices to check and regulate promiscuous behavior in the interest of human economic schemes. When we consider how universally the need of these devices is recognized, and how imperfectly they function after countless generations of trial, it seems hard to doubt that general promiscuity, conforming with behavior type No. 3, has been an experience, at some period of its evolution, of the genus to which man belongs. This racial experience, no matter when it was passed through, seems to have transmitted such a deep impression to modern mankind that it must be counted as one of the important factors that have helped to shape the social systems of today.

THE SOCIAL INFLUENCE OF RAPE

The fact that human male force can in the end be sexually effective is accepted without dispute. Doubts may arise with regard to special stories; but no one questions the essentially true nature of traditions like the Rape of the Sabines, or of old chronicles like the rape of Tamar by her half brother Amnon (*2 Samuel*, 13: 1–15) and the death of the Levite's concubine on the morning after the men of Gibeah had subjected her to a night of multiple rape (*Judges*, 19: 24–30). Still less is general skepticism aroused by newspaper accounts of the latest assault case with its subsequent lynching. But, though the reality of this kind of behavior is admitted, the considerable part that rape may well have taken in shaping human customs seems not to have received all the attention that is its due.

I have already (p. 395) tried to show how specifically human is the transfer of the final decision in sexual intercourse from the female to the male. This transfer, much though it might be welcomed by the males of other animals that are subject

to continuous spermatogenesis, appears to have become a racial characteristic of man alone among mammals because of man's high mental development combined with his extreme pelvic adaptation to the upright posture. I now wish to speak of some cultural results of this transfer. As an introduction I shall quote from Briffault (1927, vol. 2, pp. 21–22). The passage is particularly interesting because it shows how widely distributed rape is outside of our own society, and also because it indicates the manner in which social behavior begins to be influenced by this peculiar feature of human sex ways.

> The dangers of such violence are in primitive societies very real. In Australia any female found unprotected is invariably abused and often killed afterwards. In East Africa, among the Wayao and other tribes, a man, we are told, will never pass a solitary unmarried girl without entering into sexual relations with her, and if she refused he would probably kill her. So likewise among the Andaman Islanders an unmarried girl who repels a man runs the risk of being killed. Among the Siouan tribes of North America, "a man has as little control over his passions as any wild beast, and he is held as little accountable for their indiscriminate gratification." Rape was extremely common. Among the Pima Indians the young men actually used lassoes to catch any stray female they might find. Hence among the plain tribes, "custom makes it not only improper, but very dangerous for an Indian woman to be found alone away from her lodge; for an unmarried girl to be found away from her lodge alone is to invite outrage, consequently she is never sent out to cut and bring wood, nor to take care of stock." Further, it was the practice among all those tribes for unmarried girls when they went out at night to meet a lover, or to some 'dance,' to tie a rope round their thighs in such a manner that, while it did not interfere with their movements, it served as an effective preventive against violence on the part of the men.

The different types of social behavior that appear to have had their exact form influenced by masculine control of the sexual decision are chiefly of two kinds: those that resist or avoid this control and those that make use of it.

Among the customs that resist or avoid this feature of male dominance we find conventions, like those mentioned by Briffault, in which social proprieties, restrictions of feminine economic activities, and details of feminine dress, owe their origin to fear of male aggression. A careful search for customs of this kind would probably show that they are many and widely spread. Our own society is not without its social usages that seem to reflect the same fears that once beset the plains Indian squaws. Unaccompanied women, for instance, do not avoid certain districts of our cities after nightfall simply because of a supposed or real danger of robbery. The threat of sexual violence is always present in the background of this taboo as well as in the social criticism that infraction of the rule so often elicits. The peculiar behavior patterns so much talked about and written about as "animosities between the sexes" and as "feminine guiles" should also be considered. These may well have arisen, in part at least, from the common primate tendency to use sexual ruses for self protection, stimulated to specialized developments by the biologically unusual sexual dominance of the human male. It would seem highly improbable that they could ever have assumed any social importance if women, like female monkeys, possessed unquestioned sexual control of their persons by virtue of physical fact, and consequently were not subjected to an ever present conflict between the accepted fiction that they are free to choose and the never entirely forgotten reality that in the last appeal they are not.

Other social features of the same type may be detected in the strongly emotional reaction to rape in our society. As illustrations we have only to think of the frequency with which this emotion is exploited in literature, on the stage and on

the screen, and also to remember the excessive severity of legal repressive measures, and the flourishing condition of blackmail, as recently described by Robinson (1929, pp. 307–315). Throughout the southern United States the same emotion complicates the problem of social adjustment between negroes and whites; and it was appealed to for purposes of propaganda during the world war.

Passing now to the social conventions that turn male sexual dominance to account we find the many marriage customs in which the preference of the woman is slightly or not at all considered,—a long catalogue of practices that includes on the one hand such realistic items as marriage by capture or purchase, the exchanging or lending of wives, and on the other hand such now empty formalities as our own ceremony of giving away the bride by her father or by some other male relative. The pawning of women as practiced in Liberia is a frankly commercialized specialization (Strong, 1930, vol. 1, p. 70, fig. 48). Briffault (1927, vol. 3, pp. 404–405) has shown how, in Europe during the age of chivalry, the rape of an unaccompanied woman was socially condemned, whereas rape after the fair conquest of a woman's male escort was regarded with complacency. The institution of child marriage, particularly as we find it in Australia and India, with its sanctioned physical injury of small girls by adult men (See Briffault, 1927, vol. 2, p. 60; Indian Legislative Debates of 1922, vol. 3, pt. 1, appendix, p. 919; Mayo, 1931, also 1927, pp. 11–62; *Journ. Amer. Med. Assoc.*, vol. 95, p. 1188, October 16, 1930) is another social exploitation of this prerogative of the human male, coupled, however, with a somewhat unusual specialization of the primate tendency—one of the features of oestrus-free behavior—for adults to take sexual interest in individuals of prepubertal age.

In India this last peculiar item of man's primate heritage is definitely turned to social account, while in European civilization it is outlawed. Trevor Pinch, formerly editor of *The Civil and Military Gazette*, India, writes of it (1930, p. 116):

> Primarily arising from the sex-obsessions which I have already described, it is enjoined upon men, youths, and even mere boys, that they should mate with young and virgin girls. Many observers have placed it on record that this marked preference for girl-children of very tender age is a disturbing and discreditable feature of Hindu life. Still, the fact must be faced. He who would shut his eyes to it is a fool.

In France the criminal statistics covering a period of 25 years showed that there were 17,657 convictions for sexual assault on girls less than 16 years of age, while, during the same period there were only 4,360 convictions for assault on adult women (Tardieu, 1878, pp. 18–19). Exactly how much of this discrepancy arose from the better means of defense available to grown persons as compared with children is not certain; but the figures strongly suggest the existence in European men of a type of impulse closely similar to the one that moves the adult Hindu when he seeks a child wife and legally maims her.

Those types of human polygamy in which the wives are obtained through transactions between men and are afterwards held in virtual servitude may also owe their original establishment and their exact present form in some part to the specifically human male sexual dominance. In any event, such associations fundamentally differ from the polygamous groupings with which we are acquainted in other mammals, particularly in seals and ungulates. The social function of the male horse, deer, or furseal, so far as reproduction is concerned, doubtless includes some "herding" of the females, as well as some fighting off of masculine rivals. But, in these non-human sexual groupings, it is obviously the general rule that the

females at their own appropriate physiological season voluntarily accept and associate with the male and as voluntarily refuse and desert him when impregnation has been accomplished. Therefore nonprimate polygamy and the human types of polygamy in question, though they may superficially resemble each other, actually rest on unlike psychological bases; and the distinguishing characteristics of each system are exactly those that might be expected to have arisen under the contrasting influences of control of the sexual decision by the female in seals and ungulates and by the male in man. The following descriptions of two polygamous groups should make this distinction clear.

In the Alaskan furseal, one of the most extremely polygamous of mammals, the males, as we have already seen (p. 382), are the first to arrive at the breeding grounds. Because each bull must remain at his post to defend it against rivals there is no seeking and capturing of mates. When the females come to land they go of their own accord to the males, and the most that any bull can do is to seize with his teeth some cow that passes within reach. From ten to forty-eight hours after the birth of her young each female solicits reimpregnation. Concerning the female's behavior at this time and the male's subsequent attitude toward her Elliott (1884, pp. 110–111) is very definite. He says:

> The cow always makes the first advances to the bull. If she is one of the earlier subjects for his attention, the union is soon accomplished; but should she be of the later applicants in his harem, after he has been more or less exhausted by the vital drafts made upon him, she must wait. I have observed instances of this character in which the female teased the male for hours and hours before arousing him. . . . . She is satisfied [after one act of copulation], and passes rapidly out of heat. Certain it is that she is not noticed by him again; she goes up to his seraglio-grounds, to and from the sea, seeking her young and feeding undisturbed for the balance of the time; also, that the other bulls seem to recognize this condition of passed sexual requirement and satisfaction, in her case, by paying her no attention.

Perhaps the baboon harems studied by Zuckerman may present a nearer approach to human conditions than is seen in the foregoing example of animal polygamy; but the details, unfortunately, are not available at the time of going to press.

The strikingly different character of a human polygamous association is well brought out by Post Commander G. Reynaud's account (1911, pp. 870–871) of a wealthy Moroccan's harem.

> Ahmed passes for a very virtuous man because every year he joins the pilgrimage to Mecca. On arriving in Asia Minor he interrupts his pious journey to go to Constantinople and especially to Bursa, whence he brings home pretty Circassian girls purchased at a high price. He has thus built up an enchanting collection of beautiful women, which I once had the opportunity to admire. Invited to lunch at his home I was received by my host at the doorway. Three widely spaced strokes of a knocker announced to the feminine members of the household that it was time for them to disappear. The women were given the time necessary to eclipse themselves: all remained crowded in dense ranks in the colonnade-surrounded courtyard, and, after having allowed themselves to be seen, they ran riotously away. . . . . Many people think that Musulman women accept polygamy without objection. . . . . And indeed, when all dignity is debased in these unfortunate creatures on whose soul and body forcible hands have been laid, they accept with resignation the inevitable, and murmur the word of the fatalist: "Mektoub,"—*it was written*.

The custom of purdah, or strict cloistering of women, as it now exists in India, seems to rest, in some part, at least, on both the exploitation and the fear of male aggression. In describing it Katherine Mayo writes (1927, pp. 112–113):

> That view of women which makes them the proper loot of war was probably the origin of the custom of *purdah*. When a man has his women shut up within his own four walls, he can guard the door. Taking Indian evidence on the question, it appears that in

some degree the same necessity exists today. In a part of India where *purdah* but little obtains, I observed the united request of several Hindu ladies of high position that the Amusement Club for English and Indian ladies to which they belong reduce the minimum age required for membership to twelve or, better, to eleven years. This, they frankly said, was because they were afraid to leave their daughters of that age at home, even for one afternoon, without a mother's eye and accessible to the men of the family.

Far down the social scale the same anxiety is found. The Hindu peasant villager's wife will not leave her girl child at home alone for the space of an hour, being practically sure that, if she does so, the child will be ruined. I dare not affirm that this condition everywhere obtains. But I can affirm that it was brought to my attention by Indians and by Occidentals, as regulating daily life in widely separated sections of the country.

It seems difficult if not impossible to explain the origin and maintenance of social behavior patterns such as these except on the ground that, whatever strictly economic elements they may contain, they all owe important features of their exact form to the knowledge possessed by both sexes that the physical control of the sexual decision belongs, in last resort, not to the females but to the males.

SUMMARY AND CONCLUSION

The main characteristics of human sexual behavior, contrary to a widely prevalent belief, are not peculiar to man. Though they differ conspicuously from the characteristics of sexual behavior displayed by domestic ungulates and carnivores, most of them are shared by man with several non-human primates that have been subjected to comparative psychological study. In this department of his behavior man has invented nothing essentially new; the relatively unimportant human behavior patterns that have not been identified in other members of the order Primates can probably all be explained as specializations of behavior that is known to occur among non-human Old World members of the group.

Only two of these human specializations are of such a nature that they appear to have had any significance in directing the general course of cultural development. The first is that man seems to have a stronger tendency than most other primates to form continuing sexual partnerships. The second is that in man alone of all mammals is the male known to be able to force his sexual will on an unconsenting or unconscious female, a peculiarity that seems to arise from human ingenuity combined with the human pelvic adjustments to the upright posture.

These two special human features, together with two others that belong to the general primate heritage, namely, the freeing of the sexual instinct from the sharply defined physiological rhythms that direct it in other mammals, and the often rapid "fatigue of the sexual sensorimotor system through excessive stimulation by a too constant object" provide human society with some notably discordant behavioral elements. Unreasoned attempts to control these elements in the interest of varying cultural trends seem to have been the principal sources of the multitudinous systems of marriage that exist in the world today.

The fact that man's sexual behavior is not governed by sharply defined physiological rhythms gives powerful support to the view that the human societies now in existence have developed from an earlier condition of sexual promiscuity consistent with this free type of behavior. The circumstance that no societies now exist without some kind of formal marriage has little bearing on the question, because all living members of the genus *Homo* are highly specialized in the zoological sense, and all present-day societies, not excepting the less efficient ones that are usually but

misleadingly called "primitive," must therefore owe the cultural features that now distinguish them from one another to an extremely long process of evolution. That sexual promiscuity—in the sense of an habitually temporary and fluctuating association of sexual partners—is a phase ancestral to the existing social systems is further indicated by the facts (a) that marriage customs, taboos, and laws are largely attempts at curbing just such promiscuity, and (b) that both premarital and extramarital promiscuity can easily be shown to flourish in most societies, including our own.

The passing of the control of the sexual decision from the female to the male is a human peculiarity that has probably influenced many lines of social development. Some customs, such as particular standards of feminine social propriety and many restrictions of feminine activities, reflect the fear of male aggression. Others, such as those marriage customs that largely eliminate feminine preference, also child marriage by adult men, and the more specialized forms of human polygamy turn this aggressive ability to direct account.

The sexual psychology of man together with the social usages whose forms have been influenced by it can never be fully understood through the study of man alone any more than human anatomy and physiology can be so understood. It is on comparative studies that sound results must depend.

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HAPLOIDY IN METAZOA

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INTRODUCTION

THE origin of haploidy in Metazoa, its bearing on the problem of sex determination, and indeed the very existence of haploid individuals have long been the subject of much cogitation. As one or all of these questions have presented themselves in various fields of biology, different investigators have endeavored to explain the moot aspects, each from his own point of view. As a result there is available a conglomeration of hypotheses. To admit that few of these are worth consideration, and none is entirely satisfactory is in itself an appreciation of the difficulties involved. The subject as a whole has repeatedly presented itself in our work on the cytology of the coccids, and the present review has been written not only with the intention of critically evaluating the more important of the various hypotheses but also of discussing the possible bearing that certain features of coccid cytology may have on the question.

The central point of interest lies in the fact that so far as is known, all haploid animals are males. The present brief survey of the various attempts to throw light on this peculiarity and the related facts which it involves does not endeavor to go back beyond the period when the rôle played by the nucleus in the mechanism of heredity first became fully realized.

HYPOTHESES OF HAPLOIDY

Older hypotheses

Perhaps the first to consider the status of haploid individuals in this period was von Lenhossék ('03), who suggested that the queen bee carries two kinds of eggs, one of which is of a female and the other of a male type. Only the former can be fertilized, and, indeed, requires fertilization before development can occur; whereas the male type of egg develops parthenogenetically and is perhaps not fertilizable in any case. Buttel-Reepens in the very next year subjected this hypothesis of a progametic sex determination to a thorough criticism which practically eliminated it from consideration, and genetic and cytological investigations have since that day supported Buttel-Reepens. However, the ideas expressed by von Lenhossék have since reappeared in the literature several times (thus Godlewski, '13).

In 1905 and 1906 R. Hertwig proposed his hypothesis of the karyoplasmic ratio, and in the course of its elaboration also considered the question of the production of haploid males. According to Hertwig, when the eggs of the bee develop parthenogenetically after reduction there must occur a readjustment of the nuclear volume of such proportions that a karyoplasmic ratio characteristic of maleness results. But in 1912 he abandoned the hypothesis in so far as it pertained to sex determination in general and haploid parthenogenesis in particular. Indeed, shortly after this Nachtsheim ('13) and Oehninger ('13) reported the nuclear volume to be very much the same in corresponding organs of the two sexes. This of course does not eliminate the possibility that the cytoplasmic volume of female cells differs from that of male cells, which in itself would furnish a basis for a difference in

karyoplasmic ratio. However, in an entirely different insect, *Icerya purchasi*, Schrader and Hughes-Schrader ('26) have shown that even where there is a difference in the volume of chromosome material between the two sexes, the cytoplasmic volume varies proportionately. But it must be recognised that exact measurements are very difficult to make, and that a very slight difference between female and male cells may conceivably escape unnoticed, although possibly of the utmost importance in the process of sex determination. But even though it must thus be admitted that the volumetric relationship of nucleus to cytoplasm may possibly play some rôle in the question, we are not in a position to utilize the suggestion at the present moment.

Chromosomal hypotheses

This brings us to a consideration of hypotheses involving chromosomes, both from the cytological and the genetical points of view. The first of these met all the objections that had been voiced against the earlier hypotheses and rested on the original form of the sex chromosome hypothesis. As broached by Wilson ('09) and Nachtsheim ('13) it may be given briefly as follows. Each X chromosome carries a definite quantity of some substance, which we may call sex chromatin. The total quantity of sex chromatin present in the developing egg determines whether a male or a female is produced. Thus two X chromosomes contain the quantity of sex chromatin which will bring about female development; one X the quantity that results in male development. This would explain not only the normal type of sex determination of diploid animals in which females are characterized by the chromosome formula 2 A + 2 X and males by 2 A + 1 X (when A = one haploid set of autosomes), but also furnishes a simple explanation for the fact that haploid individuals are always male. For evidently if only the X chromosomes and not the autosomes are primarily responsible for the character of the sexual development, an egg which develops parthenogenetically after the reduction division has left it with only one X, would automatically give rise to a male.

The further development and elaboration of this older sex chromosome hypothesis culminated in the theory of sex determination which is embodied in the conclusions of Goldschmidt and Bridges. The chief departure of this modern theory from its progenitor lies in the recognition that autosomes as well as sex chromosomes are concerned in sex determination and that in effect the whole process rests on genetic factors just as does the development of any other character. Since in the case of Drosophila it so happens that the total effect of the genes concerned with sex determination carried by the X chromosome is to push development in the female direction, whereas that of the corresponding autosomal genes is toward maleness, sex determination may be said to rest on the ratio of the number of X chromosomes to the number of haploid sets of autosomes, which in turn may be expressed as a quotient. If this quotient is 1 or greater, femaleness is indicated; if it is .5 or less, maleness.

But although this modification of the older sex chromosome hypothesis has been triumphantly successful in meeting all the newer cytological and genetic data, it has also thrown open once more the old puzzle of sex determination in haploid individuals. For manifestly, a haploid Drosophila would have the formula 1 X + 1 A, and the quotient in that case would be 1, just as it is in the normal female of the species. Therefore if such a Droso-

phila were viable (which apparently it is not) one would expect it to be a female and not a male, as is the case with all known haploid animals.

Bridges' subsidiary evidence ('25a, '25b, '30) does indeed suggest that in Drosophila this expectation would actually be realized. Thus in certain mosaics, circumscribed regions of the fly are composed of cells which have lost most and possibly all of the chromosomes of one haploid set, and such regions appear to be female in character. If, for instance, an area of this type includes the front leg, the sex comb, which is characteristic of males only, will be absent. Now it must be recognized that the demonstration is not complete, for Bridges has not been able to show that the complete haploid set of chromosomes has been eliminated from the cells of the regions in question, but the general tendency of these findings is certainly in support of his general conclusion. But, if anything, this makes the fact that in all other cases haploid individuals are always males, only a still greater puzzle.

Schrader and Sturtevant ('23) suggested that a compromise may be brought about in the following way. If X be given the arbitrary value of -6, and A the value of $+2$, and if it is further assumed that the threshold value for femaleness is at -7 and for maleness at -5, then it is possible to regard the effective relation as an algebraic summation of the two types of chromosomes. (Apparently Witschi ('29) has taken this to mean that algebraic sums on the minus side of o connote femaleness and those on the plus side maleness. This is of course a misunderstanding of the hypothesis. As indicated above, the direction of sexual development depends on which side of the threshold values the algebraic sum falls. Since the present paper was sent to press Klingstedt (Act. Zool. Fenn. 10) has made a similar criticism of Witschi's interpretation.) In other words, with these arbitrary values, a preponderance of seven units of femaleness would bring about normal female development, whereas a preponderance of only five units would result in maleness. A comparative tabulation of the genic balance hypothesis of Bridges and the algebraic sum hypothesis side by side will show at a glance the relationship of the two (Table 1).

It will be seen that the algebraic sum hypothesis will account for the fact that haploid individuals are males, whereas the genic balance hypothesis does not. Bridges has, however, objected that, so far as Drosophila is concerned, the applicability of the algebraic sum hypothesis is dubious because the numerical differences between the successive types do not correspond very well to the actually observed differences in the sexual characters of the flies of the different types. Thus there is a difference of eight units between the diploid and the tetraploid females, which in actuality show practically no difference in their sex characteristics, whereas only six units indicate the striking difference between the females and the males. Since the genic balance hypothesis accounts for such differences very well, the algebraic hypothesis is manifestly at a disadvantage until further evidence is brought out in its support.

TABLE 1

Sex types of Drosophila analysed according to the algebraic sum and the genic balance hypotheses of sex determination

NAME	CONSTITUTION	ALGEBRAIC SUM	GENIC BALANCE
Super-male	X + 3A	0	0.33
Male	X + 2A	− 2	0.5
Haploid	X + 1A	− 4	1.0
Intersex	2X + 3A	− 6	0.66
Diploid female	2X + 2A	− 8	1.0
Triploid female	3X + 3A	−12	1.0
Super-female	3X + 2A	−14	1.5

Unlike Bridges, Goldschmidt ('20) has included in his considerations the question of sex determination in haploid individuals. Utilizing certain conclusions derived from his crosses of Lepidoptera, he suggests that the genes for maleness (MM) impress their effect upon the egg before maturation and hence all eggs are alike in their male tendency. The X-chromosome carries one or more genes for femaleness (F). If the relationship is FF > MM > F, then an explanation for the maleness of haploid individuals is at hand, since the number of X chromosomes depends on whether the egg has been fertilized or not. If fertilized, two X are present and the female tendency thereby dominates the male tendency. But if not fertilized, only one X is carried in the egg and then the male tendency gains the upper hand. Goldschmidt's hypothesis thus makes due allowance for the existence of haploid males. It need hardly be said that it would at once gain the utmost importance if further light could be thrown on the rôle that Goldschmidt ascribes to the cytoplasm.

Other hypotheses

No immediate solution of the difficulties involved in the problem is to be expected from the suggestions recently made by some other workers. Thus Witschi ('29) has suggested that since the diploid individuals in our cases are always females, the factors for femaleness must there be epistatic to those for maleness (i.e., FF > MM). But since haploid animals are always males, the explanation may rest on the fact that the haploid state in some way changes the conditions obtaining in the diploid individuals and thus M > F. It may well be assumed that if such a reversal of epistatis is responsible for the maleness it in turn is due to physiological conditions obtaining in haploid individuals. But that, of course, is not an explanation and merely serves as a basis for the opinion that a final elucidation must rest upon an experimental analysis of such physiological conditions. Indeed Witschi himself is free to state that he regards this interpretation merely as a suggestion for further work.

Nor does Castle's recent proposal ('30) that the interpretation of several workers on sex determination in lower plants be applied to animals offer immediate help, and this despite the fact that Castle had haploid animals especially in mind. As is well known, the interpretations just mentioned are based on the supposition that sex differences are merely plus and minus variations in a single scale of gradations in sexual character. In the sex determination of animals like Drosophila we are dealing with two types of individuals, those with a plus and those with a minus tendency, or male and female respectively. The mature eggs all being alike in carrying the plus tendency, the production of two sexes must of necessity rest upon the existence of two kinds of sperm. As is already well known, this differentiation rests on the so-called X Y chromosomes, the X being considered as a chromosome with a plus or female tendency, while the Y is neuter or else of a minus tendency. All that is of course nothing more than a slightly different way of stating what we already know. But it is quite clear that on this basis, if an egg is not fertilized and develops parthenogenetically it can carry only the plus or female tendency. In other words, Castle encounters exactly the same difficulty as does Bridges in the latter's conception of the genic balance hypothesis, for according to this view a haploid individual should be female and not male.

Castle is of course aware of the difficulty and endeavors to escape the dilemma by

suggesting that in such a haploid individual "its feebler haploid state (perhaps) causes it to form sperms rather than eggs but these sperms transmit the plus sex-tendency for which the mother was homozygous." The hollowness of this explanation is manifest, and indeed seems to be apparent to Castle himself, for a few lines farther on he writes as follows: "What makes these haploid individuals somatically male (producers of sperm rather than eggs), we are at present unable to state. Genetically they are female; phenotypically or somatically only are they male." Needless to say the sentences just quoted are tantamount to a concession that we are just where we were before.

In brief, none of the present hypotheses is fully satisfactory, Of them all, only Goldschmidt's and Schrader and Sturtevant's will cover both diploid and haploid males. The former of these is in urgent need of further elucidation of the basic assumption that maleness can be impressed upon the cytoplasm of the egg before fertilization, whereas the latter offers a conflict with the genic balance hypothesis which affects at least its general applicability.

OCCURRENCE OF HAPLOIDY IN METAZOA

Criteria of haploidy

Before considering our own suggestions in their relation to the various aspects of the problem of haploidy, it may not be amiss to take stock of our present knowledge concerning the occurrence of species with haploid males. Although the number of species in which haploidy occurs is probably much larger than was formerly thought, a satisfactory demonstration of its existence has so far been given in relatively few instances.

It must be realized that such a demonstration cannot be made without cytological evidence. Breeding experiments alone may well establish that females are capable of producing young without fertilization by a male and that the young so produced are invariably males. Again, genetic evidence may show that such offspring are always homozygous. But neither the one nor both of these findings is sufficient for a demonstration of haploidy, for such evidence in no wise precludes the possibility that diploidy has been restored to the developing egg by any one of several methods. Thus the eggs might undergo a reduction division and, if this were followed by a separation of the equational halves of the chromosomes unaccompanied by a cytoplasmic division, development would take place in a homozygous condition but with the diploid instead of the haploid complement of chromosomes.

Indeed, if cytological evidence to the effect that the eggs actually do undergo a normal reduction be added to the genetic evidence, haploidy is still not necessarily implied. Thus in the facultatively parthenogenetic race of Lecanium studied by Thomsen ('27), all eggs undergo a normal maturation, but diploidy is restored to the unfertilized eggs by the secondary union of the second polar body nucleus with the female pronucleus. Were the first maturation division reductional in this case, the parthenogenetically produced young might be homozygous for characters heterozygous in the mother, and still have been diploid throughout their entire development.

Similarly, if Tauson's ('27) evidence on *Asplanchna intermedia*, and Doncaster and Cannon's ('20) on Pediculus, are to be believed, an investigation of the spermatocytes need not in itself give a decisive test for the presence or absence of haploidy, for a precocious reduction may occur earlier, as in the spermatogonial cells.

TABLE 2

Forms in which the haploidy of males has been completely demonstrated. Abbreviations as follows: clv.—cleavage, dip.—diploid, div.—division, embr.—embryos, hap.—haploid, mat.—maturation, nucl.—nucleus, oog.—oogonia, pronucl.—pronucleus, soma.—somatic cells, spcyt.—spermatocyte, spg.—spermatogonia, sptid.—spermatid

SPECIES	BREEDING DATA	NON-MEIOTIC CHROMOSOMES		MEIOSIS		REFERENCE	REMARKS
		♀	♂	♀	♂		
ACARINA							
1. *Tetranychus bimaculatus*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	6 in fusion nucl., clv. nucl., embr., & soma. & oog. of nymphs.	3 in ♀ pronucl., clv. nucl., embr., spg., & soma. of young nymphs.	2 mat. div. → hap. pronucl.	Probably one div. only—equational. No reduction div.	Schrader, '23	Meiotic div. not distinguishable from spermatogonial. Last div. before sptid. formation is equational.
ALEYRODIDAE							
2. *Aleurodes proletella*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	26 in fusion nucl., clv. nucl., & soma. of larvae.	13 in ♀ pronucl., clv. nucl., embr., & soma. of larvae, spg. *circa* 13.	2 mat. div. → hap. pronucl.	One div. only,—equational.	Thomsen, '27	Spcyt. div. is distinguishable from spg. div.
3. *Trialeurodes vaporariorum*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	22 in clv. nucl., embr. & soma. of pupae, oog. *circa* 22.	11 in clv. nucl., embr. & soma. of pupae, spg. *circa* 11.	2 mat. div. → hap. pronucl.	Probably one div. only—equational. No reduction div.	Schrader, '20; Thomsen, '27	Meiotic div. not distinguishable from spermatogonial. Last div. before sptid. formation is equational.
COCCIDAE							
4. *Echinicerya anomola*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	4 in clv. nucl., embr., oog., & soma. of all instars	2 in clv. nucl., embr. spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only,—equational.	Hughes-Schrader, '30	
5. *Icerya litteralis*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	4 in clv. nucl., embr., oog., & soma. of all instars.	2 in clv. nucl., embr. spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only,—equational.	Hughes-Schrader, '30	
6. *Icerya montser-*	Virgin ♀ ♀→♂♂	4	2	2 mat. div. →	One div. only—	Hughes-Schrader,	

		stars.	nymphal instars.				

6. *Icerya montserratensis*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	4 in clv. nucl., embr., oog., & soma. of all instars.	2 in clv. nucl., embr., spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only,—equational.	Hughes-Schrader, '30	
7. *Icerya purchasi*	Unmated ♀ ♀ → ♂♂ & ♀ ♀ Mated ♀ ♀→♂♂ & ♀ ♀	4 in fusion nucl., clv. nucl., embr., oog., & soma. of all instars.	2 in ♀ pronucl., clv. nucl., embr., spg., & soma. of all nymphal instars.	2 mat. div. → hap. pronucl.	One div. only,—equational.	Pierantoni, '12, '14; Hughes-Schrader, '25, '26, '27; Schrader & Hughes-Schrader, '26	
HYMENOPTERA							
8. *Apis mellifica*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	32 in 1st clv. nucl. & embr.—may break up into 64 in late embr. & reunite into 16 in oog.	16 in 1st clv. nucl., & embr.—may break up into 32 or 64 in late embr. Spg. 16.	2 mat. div. → hap. pronucl. of 8 double chromosomes	First div. abortive. Second div. equational & unequal. Only one sptid. is functional.	Petrunkewitsch, '01; Meves, '04, '07; Doncaster, '06, '07; Mark & Copeland, '06; Nachtsheim, '13	All data from Nachtsheim. No agreement among authors as to counts or meaning.
9. *Paracopidosomopsis floridanus*	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♀ ♀ only with occasional mixed broods.	16 in clv. nucl., embr. & soma.	8 in spg. & soma.	2 mat. div. → hap. pronucl.	First div. abortive. Second div. equational & equal. Both sptids. functional.	Patterson, '17, '21; Patterson & Porter, '17; Patterson & Hamlett, '25	Report ♂ soma. "hap. with variations" which are unexplained. Haploidy established for ♂♂ of mixed as well as unisexual broods.
10. *Pteronidea ribesii* (= *Nematus ribesii*)	Virgin ♀ ♀→♂♂ only Mated ♀ ♀→♂♂ & ♀ ♀	16 in oog., *circa* 16 in fusion nucl., embr. & soma.	8 in embr. & soma.	2 mat. div. → hap. pronucl.	First div. abortive. Second div. equational & equal. Both sptids. functional.	Doncaster, '06, '07; Peacock & Sanderson, '31	All data from Peacock & Sanderson. Variability in counts of ♀ soma. & pairing of oog. chromosomes suggest "*Sammelchromosomen.*" Evidence for first div. inadequate.

The ensuing meiosis may be, therefore, of the haploid type, although the males are somatically diploid.

Finally, the possibility that haploid nuclei may double their chromosomes at some stage is always to be considered. Paula Hertwig ('20) suggested such a possibility in her consideration of haploidy in bees, and indeed just such a restoration of diploidy has since been discovered in the parthenogenetically produced frogs studied by Parmenter ('20, '25, '26). In these cases the regulation from haploidy to diploidy may occur over a considerable developmental period; only those individuals surviving, apparently, which successfully assume the diploid condition.

Thus in a given case the knowledge that males only are produced parthenogenetically from reduced or haploid eggs, and that the meiosis of the males evinces those peculiarities conditioned by the presence of but one haploid set of chromosomes, may strongly support the hypothesis of haploidy, but does not in itself prove it. The final proof must include a demonstration of haploidy in the somatic cells of the most important developmental stages of the male from egg to adult. It is with this strict but nevertheless fair criterion of haploidy in mind that we present the following analysis of the various reputed cases of haploidy among the metazoa. Fully conforming to our requirements for haploidy are the cases brought together in Table 2.

Fully established cases

It will be seen from Table 2 that in at least seven species (numbers 1 to 7 inclusive) the evidence for male haploidy is absolutely conclusive. In the three other species (all Hymenoptera) also included in Table 2 we believe the existence of haploidy to be established, but in none of these cases is the demonstration so unquestionable as in the former group. In Peacock and Sanderson's ('31) study of the saw-fly, *Pteronidea ribesii*, the most exacting criteria for haploidy would seem to have been met. But even here the chromosomes of the female line show some indication of a compound character (note the variation of the somatic counts in female embryos, and the pairing of the oogonial chromosomes). However, these variations seem in no wise to affect the chromosomes of the male line nor the basic relation between the chromosomes of the two sexes. Again, the case for haploidy in Paracopidosomopsis is weakened, although probably not materially, by Patterson and Porter's ('17) preliminary report of the occurrence of variations in the haploid counts in male somatic cells, variations which the authors have neither described nor explained in subsequent publications. Finally in the classic case of the bee, although Nachtsheim's studies have unified the conflicting reports of the many previous workers and make the haploidy of the males almost certain, the evidence may still be questioned at certain points. Thus it has been suggested (P. Hertwig, '20; Vandel, '31) that the formation of compounds or "*Sammelchromosomen*" may mask a restitution of diploidy in some developmental stage in the haploid male. This might be followed by a reduction to haploidy in the spermatogonial cells of the male. Following such assumptions (for which, it must be remembered, positive cytological evidence is quite lacking), neither the typically haploid character of the male meiosis nor the development of males from unfertilized, reduced eggs would constitute adequate evidence for the haploidy of the males, which might still be diploid during the major part of their lives. Some skepticism is perhaps justified on the grounds of the admittedly involved chro-

mosomal behavior and the highly unfavorable nature of the material for a convincing cytological analysis. In such a case the critical judgment of so skilled an observer as Nachtsheim carries more than ordinary weight, and the present authors believe his final conclusion for male haploidy to be justified.

Incompletely established cases

Table 3 brings together seven species, in each of which some cytological evidence for male haploidy is available, but in none of which has a satisfactory demonstration been accomplished. *Vespa crabo*, *Vespa maculata*, *Camponotus herculeanus*, and *Xylocopa violacea* all evince a typically haploid meiosis in the male, but data on female meiosis, on the results of breeding, and, what is especially pertinent, somatic counts in the two sexes, are either entirely lacking or quite inadequate to establish the haploidy of the males from egg to adult. *Dryophanta erinacei* is in the same situation; its case is further complicated by the fact that the only chromosome count available for the female is approximately the same as those found in the male. For *Pteronidea melanoplus* the breeding data and the type of male meiosis suggest haploidy of the males, but the absence of data on the meiosis of the egg and on the somatic chromosomes precludes a positive conclusion. In *Crypticerya rosae*, on the other hand, somatic haploidy is established for half the embryos and first instar nymphs, female diploidy is also proved, and the reduction of all eggs is very probable; lacking are late nymphal and adult male counts, and the character of the meiosis in the male.

There remains a group of species for which haploidy has been claimed on cytological grounds but in regard to which no conclusion is at present justified. The gall-fly *Neuroterus lenticularis* (Doncaster, '10, '11, '16) belongs in this category. On the basis of Doncaster's studies it is probable that the male meiosis is of the same haploid type exemplified by Paracopidosomopsis and Vespa, and that the eggs of certain females (presumably male-producers) undergo a chromosome reduction, but the observations on the chromosome cycle are too confused and contradictory to warrant any conclusion. Similarly, in *Osmia cornuta*, Armbruster found but one meiotic division in the male germ cells,—evidence of possible haploidy. Armbruster's claim that this division is reductional in character has not been confirmed, and it is probable that the apparent reduction, as well as his conflicting chromosome counts in male somatic cells, depends upon some sort of compound chromosome formation. The parasitic wasp, *Habrobracon brevicornis*, must also, for the present at least, remain in the unproved category. In 1918 P. W. Whiting made a preliminary announcement on the cytology of this wasp in which he states that the males are haploid and that one of their meiotic divisions is abortive. A. R. Whiting ('27a, '27b) confirms these general statements and adds that the second meiotic division in the male is equational and equal, and that the chromosome number is approximately 11 in the male and 22 in the female. So far, however, the cytological findings on which these claims are based have not been published and it is accordingly impossible to judge whether somatic and meiotic haploidy is actually established. A suspended judgment is especially advisable here in view of the genetic evidence for the existence of bi-parental or diploid males in this species (A. R. Whiting, '27a, '27b). The cytology of these aberrant males has not been reported beyond a statement to the effect that their meiosis seems to resemble, in the presence of an abortive first division, that of the uni-

TABLE 3

Forms in which the cytological evidence for male haploidy is incomplete in from one to almost all respects. Abbreviations as in Table 2

SPECIES	BREEDING DATA	NON-MEIOTIC CHROMOSOMES		MEIOSIS		REFERENCE	REMARKS
		♀	♂	♀	♂		
COCCIDAE							
1. *Crypticerya rosae*		4 in clv. nucl., embr., 1st instar larvae, & soma. of adult.	2 in clv. nucl., embr., & 1st instar larvae.	Stages incomplete, but 2 mat. div. indicated.		Hughes-Schrader, '30	Somatic haploidy of ♂♂ not completely proved; ♂ meiosis lacking.
HYMENOPTERA							
2. *Camponotus herculeanus*					First div. abortive. Second div. equational & equal. Both sptids. functional.	Lams, '08	Hap. type of ♂ meiosis only evidence for ♂ haploidy.
3. *Dryophanta erinacei*		13 or 14 in follicular cells of ovary.	12 in soma.		First div. abortive. Second div. equational & equal. Both sptids. functional.	Wieman, '15	Follicular counts known to be variable in other species; hap. type of ♂ meiosis only evidence for ♂ haploidy.
4. *Pteronidea melanoplus* (= *Nematus melanoplus*)	Virgin ♀♀ → ♂♂ only Mated ♀♀ → ♂♂ & ♀♀		8 in spg.		First div. abortive. Second div. equational & equal. Both sptids. functional.	Peacock, '25; Peacock & Sanderson, '31	All data from '31 paper, which corrects '25 account of 2 equational divs. Somatic chromosomes of ♂ & ♀ lacking.

5. *Vespa crabo*					First div. abortive. Second div. equational & equal. Both sptids. functional.	Meves & Duesberg, '08	Hap. type of ♂ meiosis only evidence for ♂ haploidy.
6. *Vespa maculata*					First div. abortive. Second div. equational & equal. Both sptids. functional.	Mark & Copeland, '07	Hap. type of ♂ meiosis only evidence for ♂ haploidy.
7. *Xylocopa violacea*		32 in first clv. nucl. in some eggs, presumably ♀-producing.	16 in first clv. nucl. in some eggs, presumably ♂-producing.		First div. abortive. Second div. equational & unequal. Only one sptid. functional.	Granata, '09, '13	Somatic determinations incomplete, & all data for ♀ lacking.

parental or haploid males,—a finding which, if confirmed, can only increase the need for a complete cytological study. The verdict of unproved must be passed also upon Patterson's ('28a, '28b) claim for male haploidy in the various species of Cynipidae which he has investigated, since no cytological evidence has as yet been published relative to these species.

Despite the unanimity with which previous writers have placed the rotifers in such lists, we do not regard haploidy as established there. The data from breeding experiments and the cytological evidence are sufficient to establish the fact that sexual eggs may develop parthenogenetically after giving off two polar bodies, and that such eggs always give rise to males. But no conclusive evidence is available to show that the haploid number is actually maintained. Indeed the reports of the different investigators are so much at variance with each other that it seems a matter of surprise that any final conclusion has been based on them at all. To justify this critical attitude, it may be well to review very briefly the investigations that have been made on the two genera, Hydatina and Asplanchna.

In *Hydatina senta*, Lenssen ('98) gave the diploid number as 10 or 12. In 1909 Whitney reported it as between 20 and 30, giving the haploid number as from 10 to 14. But Shull in 1921 concluded that the diploid number is 12. It will be seen that, far from establishing the fact that the males are haploid, these data do not even permit a conclusion on the diploid number.

In *Asplanchna intermedia*, Whitney ('24) reported 52 chromosomes in the female and 26 in the mature sexual egg (which gives rise to a male if unfertilized). In the same year Tauson reported the diploid number in the same species to be 24 and emphasized her conclusion that the male is not haploid. However in 1925 Wiggenhorn and Whitney supported Whitney's earlier findings with the claim that somatic cells of female embryos carry about 51 chromosomes, whereas those of males show 25 or 26. But Tauson in 1927 reiterated that the diploid number is 24 and that males are diploid and not haploid. Finally in 1929 Whitney conceded that he had misinterpreted some of the stages but did not specify in what respects he had been in error. Manifestly a final conclusion is even less justified here than in the case of Hydatina.

Nor do the remaining cytological studies on rotifers settle the question. In his apparently reliable investigation of *Asplanchna amphora*, Whitney ('29) found that the diploid number is 26 and that males are haploid. It is consequently somewhat of a surprise to read his statement that "as the chromosome cycle is very similar to, if not identical with, that of *Asplanchna intermedia*, most of the important features of Tauson's work have been confirmed," for certainly the two investigations come to no agreement on the fundamental questions of haploidy. Again, Storch's work ('24) on *Asplanchna priodonta* led him to the conclusion that the diploid number is 16 and that the unfertilized egg begins its parthenogenetic development with 8 chromosomes. (Whitney ('29) objects that certain of Storch's figures show 40 to 49 chromosomes, but he has overlooked Storch's explanation that such figures were drawn from total preparations. In these, according to Storch, the relatively long chromosomes cross and overlap each other at many points and at such localities present areas of refraction which simulate a high number of chromosomes.) But Storch was not primarily interested in the question of chromosome number, and his findings will hardly suffice to settle the matter.

No special mention need be made of the

investigations of the spermatogenesis of various rotifers except to indicate that there also no agreement has been achieved.

In judging all these findings it is only fair to acknowledge that the group presents the utmost difficulties to cytological work. But plainly, on the basis of such reports as we have reviewed, a judicial skepticism is called for, even though it seems probable that male rotifers will eventually prove to be haploid, as almost everyone now assumes.

THE COCCIDAE IN RELATION TO HAPLOIDY

Analysis of problem

There is a strong possibility that the problem of haploidy is more complex than a statement of its central point,—i.e., why are haploid individuals always male? —would suggest. The historical hypotheses of haploidy hold in common the idea that the process of sex determination in haploid individuals differs from the more usual type only in some simple or perhaps single respect. It may therefore be pertinent to suggest that the differences between the two types may well be more far-reaching and that they have not been attained in a single step. The problems which are probably involved may conveniently be placed under three headings.

1. In the first place it must be recognised that so far as we know animals which normally are diploid in both sexes do not produce viable haploid offspring. Eggs with only the haploid complement of chromosomes have been known to begin development, but never does such development go beyond the very early stages without some type of adjustment of the chromosome number. No haploid individual has ever been known to reach sexual maturity in such cases. This is especially well illustrated by researches on frogs which have been produced through artificial parthenogenesis (Hovasse, '22; Parmenter, '20, '25, '26). Since species with haploid males have undoubtedly been derived from species in which they are diploid, certain changes must have occurred to make viability in the haploid state possible. It must also be recognized that the production of haploid individuals may not have been the result of a single accident of development, as is apparently the case in the plants mentioned below, but may represent the culmination of a whole series of minor changes. The latter possibility we believe to be exemplified by certain species of coccids.

2. Among the higher plants, whose sporophytes are as fundamentally diploid in character as is the soma of the vast majority of metazoans, there appears to be no such block to the development of occasional haploid offspring. Thus haploid individuals of certain species of Datura, Nicotianum, Oenothera, Triticum, Solanum, and others have proved capable of developing to maturity with the single complement of chromosomes. But such haploid forms as these present another bar to the permanent establishment of haploidy in a species. This lies in the behavior of the single set of chromosomes during meiosis. In all the cases investigated the large majority of the pollen mother cells undergoes an irregular reduction division in which the chromosomes of the haploid group are distributed at random to the two poles. Very few male gametes therefore receive the full haploid set and become normal pollen grains. In the others the number of chromosomes may of course vary from zero to the haploid number, and such gametes are rarely if ever functional. The maintenance of the race must rest in such cases on precariously few gametes. In other words, in the evolution of a species with haploid males, the meiotic

divisions in the latter must become subject to some regulatory factor which either sends the complete haploid set of chromosomes to one pole in the reduction division, or else eliminates reduction altogether. The haploid sporophytes of the plants mentioned have not successfully overcome this second block to a permanent haploidy.

3. Even if, through the agency of such a regulatory factor, a majority of the male gametes should become functional, another obstacle remains to be overcome. A brief consideration will make it evident that since all such viable gametes of haploid individuals carry the full haploid set of chromosomes, the ensuing fertilization will at once restore the diploid number of chromosomes, and therewith haploidy disappears once more. In order to avoid this, a further change relative to the physiology of the eggs must occur to make the continuous production of haploid individuals possible. This might happen in a variety of ways. Thus apyrene sperm, or sperm carrying no chromosomes, might be produced which would nevertheless retain the ability to activate the egg; or the eggs not reached by sperm might become directly capable of independent or parthenogenetic development. However instigated, the induction of parthenogenetic development in the eggs is a third essential step in the origin of haploidy.

4. The three foregoing considerations are concerned with the mode of origin of haploidy. It will be seen that the central point of why such haploid individuals should always be of the male sex still remains. It is, however, more than probable that with a complete elucidation of the origin of haploidy this final question will be automatically answered. If our conclusions still fall short of that desideratum it must be realized that the defect lies in the fact that our analysis of the origin of haploidy is still incomplete. However, in so far as these investigations offer an approach to the central objective, they may have accomplished something toward its final solution.

Acquisition of viability in the haploid state

Within the group of the coccids are represented both beginning and end stages in the establishment of haploidy. Thus in all the iceryine coccids thus far studied cytologically, the haploidy of the males has been completely established. In all five species (representing three genera of this tribe) the cytological conditions are exceptionally clear and convincing; the females are diploid with a chromosome number of 4, and the males in every case haploid with the reduced chromosome number of 2. The viability of haploid individuals is, in these species, beyond any question. At the other extreme we find species, such as Llaveia and Protortonia, in which both sexes are invariably diploid. The expectation of finding species, within this group, representative of intermediate stages does not, therefore, seem entirely unjustified. But in no case, in the course of considerable breeding and cytological examination of Protortonia and other diploid species, has an occasional or accidental haploid form ever been encountered. In these very same cases, however, there lies indirect evidence that the ability to develop and to survive in the haploid condition is in process of acquisition by the male sex, not, as might at first be expected, by the sudden or accidental parthenogenetic development of a mature egg, but by a series of changes in the chromosomal conditions of the diploid males themselves. The evidence for this hypothesis lies in an apparently progressive degeneration in one-half of the chromosomes of the male. Different stages in this process are exemplified by different species, and it is pos-

sible so to arrange these species as to illustrate a series of steps which may have been taken in the passage from diploidy to haploidy. The basic phenomenon, as indicated above, is a gradual degeneration of one haploid set of chromosomes in the male; the process is reflected chiefly in the behavior of the chromosomes during meiosis, but in its later stages the soma also is affected.

In ordinary cases the stability and permanence of the diploid condition is dependent upon the regularity of pairing (pseudoreduction) between homologous chromosomes and the ensuing reduction in the meiotic divisions of the germ cells. In turn this pairing may be looked on as an indication that the members of the pair are homologous, any decided difference in either member affecting the synaptic relation. It is not surprising, therefore, to find that it is precisely this feature of meiosis which is first impaired by the degenerative changes leading toward haploidy. It is recognized of course that such impairment or loss of synapsis in a diploid set of chromosomes may conceivably be due to one of several causes. That in the case of the coccids it is intimately associated with the progressive degeneration of one set of chromosomes, may be indicated, we believe, by the following considerations.

The starting point in the series, i.e., the normal diploid condition with no trace of a haploid tendency, is furnished by *Llaveia bouvari*. The chromosome cycle in this species is prototypal; both sexes are diploid, the female with six chromosomes, the male with five; these chromosomes are distinguishable as three pairs of differing size, the longest pair being represented by but one chromosome in the male group. In the meiosis of the male germ cells some 95 per cent of the primary spermatocytes show the occurrence of pseudoreduction, or pairing between the members of the two pairs of autosomes. The prophase nucleus subdivides into three nuclear vesicles, in one of which the unmated heterochromosome evolves alone and precociously, undergoes an equational split, and condenses into a dyad. In each of the other two vesicles the two members of one autosomal pair of chromosomes are formed; each splits equationally and then pairs with its mate to form a tetrad. The two tetrads and the dyad divide equally at the first division. In the second division prophase the X-chromatid becomes attached to one end of the larger dyad, and in the ensuing division passes undivided to one pole, while the two autosomal dyads divide evenly. Thus two types of sperm are produced, male-determining with two chromosomes, and female-determining with three chromosomes. We would again emphasize the orthodox behavior of the chromosomes in this meiosis as probably representing the primitive or basic condition, in which the homology of the chromosomes is unimpaired and there is consequently a normal pairing and reduction.

A significant variation of this normal synapsis occurs in approximately 5 per cent of the primary spermatocytes of all the males of *Llaveia bouvari* studied, a variation which shows the beginning of the asynaptic habit. In these cells the two members of the smaller pair of autosomes evolve in separate vesicles; each one splits equationally and condenses into a dyad without any contact with its homologous chromosome. In the first division these two divide quite independently of each other. In the second division their derivative chromatids come together momentarily before passing to opposite poles. In other words, in some 5 per cent of the spermatocytes, one pair of chromosomes no longer undergoes the normal prophase

synapsis and tetrad formation,—an aberration which foreshadows the complete loss of synapsis in the males of the higher coccids and indicates the possible first step in those changes which we believe lead to the final degeneration and loss of one whole haploid set of chromosomes.

In *Protortonia primitiva* the progressive impairment of synapsis in the male line is much further advanced. The somatic chromosome situation resembles that in Llaveia; the females have a diploid set of six chromosomes, the males of five, of which only the heterochromosome of the male and the corresponding pair of the female set, are distinguishable by their size. In the primary spermatocytes no pairing of the ordinary sort occurs. Four nuclear vesicles are formed. A single chromosome develops in each of three of them. In the fourth and largest vesicle, two chromosomes are formed, but except for a transient, possible, end-to-end contact between two of the four equational halves or chromatids of these (all the chromosomes in this division show a precocious and exaggerated separation of their equational halves) as they line up into a row of four units prior to the division, no actual pairing or synapsis occurs even between these two chromosomes. The retention of the common vesicle, together with the persistence of some degree of contact between the chromosome mates, we interpret as remnants of an old synaptic behavior. Comparison with Llaveia strengthens this interpretation, for there in 95 per cent of the spermatocytes each chromosome pair evolves within a single vesicle and there undergoes a regular synapsis and tetrad formation. Similarly, the type of behavior found in the aberrant spermatocytes of Llaveia, with their individual vesicles for each of the members of one chromosome pair and the accompanying loss of synapsis by this pair, has become the invariable rule for all but one pair of the Protortonia chromosomes. These relations are graphically represented in figure 1, which gives in diagrammatic form the three metaphase configurations resulting from the three

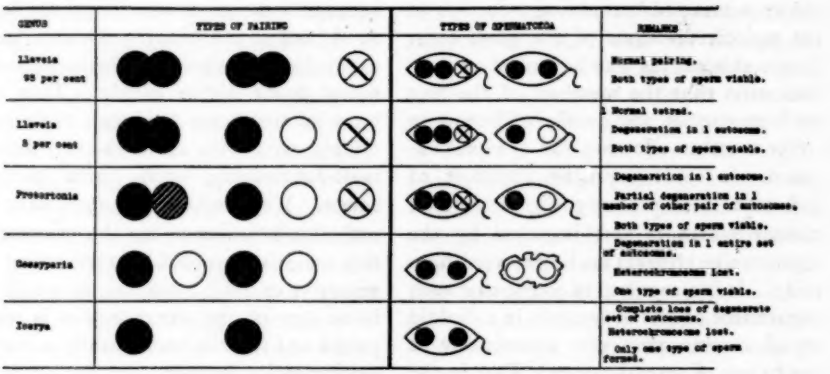

FIG. 1. DIAGRAM SHOWING PROGRESSIVE DEGENERATION IN ONE HAPLOID SET OF CHROMOSOMES, AS ILLUSTRATED IN A SERIES OF DIFFERENT SPECIES

Tetrad formation indicated by partial merging of two spheres or chromosomes, and partial loss of synapsis by apposition without merging. Normal chromosomes black, partially degenerate chromosomes striped, and completely degenerate chromosomes white. Heterochromosome indicated by X.

types of chromosome behavior just described. It will be seen that the progressive loss of synapsis and the accompanying separation of the once homologous chromosomes is the basic factor underlying the differentiation of the three types, which thus represent three closely seriated stages in a common evolution.

Passing now to the case of Pseudococcus—the three species which have been investigated show such uniformity of chromosome behavior that they may be discussed as a unit—, we encounter a type in which asynapsis is fully established for all the chromosomes, in all the cells of the male germ line. The females show a diploid set of ten chromosomes, and, as in all the other cases, a completely orthodox behavior. The male diploid number is also ten, but one of the two haploid sets of chromosomes tends to remain partially condensed and clumped during the resting phases of the nuclei. In the primary spermatocytes this haploid set condenses in advance of the other set, and, after a first division equational in character for all ten chromosomes, the telophase nuclei still show a differentiation and segregation of the chromosomes into two groups, one clumped and one loosely aggregated. The second division effects a separation of these two haploid sets, one passing to each pole. The points pertinent to the present discussion are the complete absence of synapsis, and the associated lack of synchrony in the cyclic changes of form in the chromosomes of the two haploid sets. A third point of interest is the fact that the changes undergone by one haploid set of chromosomes are reflected in the somatic, as well as the germinal, cells of the males. That haploid set which condenses precociously and tends to clump and act as a unit in the meiotic divisions, may be recognized in the somatic nuclei of all except the earliest developmental stages by similar although less strongly marked characteristics.

In *Gossyparia spuria* we find a still more radical change in one haploid set of chromosomes of the male. Moreover, in this case there is strong evidence that these changes are positively degenerative in character. As usual the female is a normal diploid, with a chromosome number in this case of 28. In the meiosis of the male germ cells the behavior of the two haploid sets of chromosomes is remarkably different. One haploid set shows a marked heteropycnosis in the primary spermatocyte prophases, and this is accompanied by a peculiar pairing of its chromosomes. This pairing is not, apparently, of a synaptic nature; the fact that it is preceded by no preliminary formation of chromosome threads, together with occurrence of slight variations in the numbers of the bivalents formed, indicates the aberrant character of the association. The second haploid set evolves more slowly in the primary spermatocyte prophases. Its chromosomes, strikingly enough, show no trace of pairing, and give every indication of a normal condition. The first division is equational in the sense that all fourteen of the chromosomes of the normal set and the seven bivalents of the heteropycnotic set all undergo division. The condensation of the heteropycnotic group is maintained throughout the interkinesis, and the second division effects the separation of this group from the normal one. Finally, and this point clinches the evidence for the degenerative nature of the peculiarities of the heteropycnotic chromosomes, those spermatid nuclei which receive them almost invariably disintegrate; only those spermatids which receive the normal haploid set of chromosomes form functional sperm. Among thirty individuals studied, only one showed any attempt on the

part of the degenerate nuclei at sperm formation; and in this case the sperm formed were of a highly abnormal type. This exceptional case adds weight to the conception that the heteropycnotic chromosomes represent a group which formerly formed sperm but which has lost this ability through progressive degeneration, for it may possibly represent the occasional persistence of a stage just prior to the condition reached by the majority of the Gossyparia males in the evolutionary process in question.

The peculiarities of the heteropycnotic chromosomes are not an exclusively meiotic phenomenon, but find expression in the somatic cells as well. The abnormality of one haploid set of chromosomes becomes visible somatically for the first time during the late blastula stage in the development of the male individual. From this point on, the heteropycnosis and persistent condensation and clumping of one group of chromosomes continue throughout both resting and division phases of the somatic nuclei. It thus seems highly probable that Gossyparia males are, therefore, haploid in effect from an early developmental stage on, due to the inactivation of one haploid set of their diploid chromosome complement.

Such a series of changes as we have outlined, indicating a progressive physiological inactivation of one chromosome set, would logically culminate in the complete morphological loss of this haploid set from the chromosome cycle of the male. This final stage is indeed realized in the coccids by various of the iceryine species (Icerya, Echinicerya, and Crypticerya). In these forms, as described earlier, the morphological haploidy of the males is completely established.

To summarize, we submit that the gradual establishment of asynapsis, followed by increasing impairment of the synchronous functioning of the two haploid sets of chromosomes, is correlated with the progressive degeneration and final loss of one set of chromosomes. Ability to survive in the haploid state may thus be in process of acquisition by the males of certain species of coccids, as it is already attained by others. A diagrammatic representation of the possible steps involved in this process as illustrated by the different species of coccids just discussed is shown in figure 1. It cannot be too strongly emphasized that this scheme attempts no expression of the phylogenetic relations of the various coccid species involved. This is indeed obvious, since Icerya, here regarded as a possible final stage, is certainly far more primitive, and more closely allied to such basic forms as Llaveia, than are the highly specialized species of the Gossyparia and Pseudococcus groups. The evidence is rather to be interpreted to the effect that some such development as we have traced is taking place in different groups of coccids, but evidently at different rates, and probably in different ways, in different groups. Thus in the specialized Lecanium species studied by Thomsen ('27)—the males in these species are very like Pseudococcus in their cytology—the development of a diploid female-producing parthenogenesis in the female line may well result in the gradual loss of the males from the species, rather than, or before, the assumption of haploidy by them. Similarly in one species of Icerya, *Icerya purchasi*, the development of a functional hermaphroditism in the female line, in this case probably subsequent to the establishment of haploidy in the males, seems to be resulting in a marked decrease in the numbers of males in this species, which may well be preparatory to their final complete loss from the species.

Regulation of the reduction division in haploids

If, as we have postulated, the gradual development of male haploidy involves a progressive degeneration on the part of half of the chromosomes and if this degeneration involves first the impairment and then the loss of synapsis, then those species undergoing this evolution must simultaneously acquire a regulative mechanism which will prohibit the random distribution of the normal and the degenerating chromosomes. For it will be recognized that in order to maintain completely functional gametes, the normal chromosomes must be separated from the abnormal in the reduction division. The cytological evidence for such progressive regulation may be presented as follows.

In Llaveia the normal mechanism still obtains. Synapsis and pseudoreduction occur and are followed by a reduction division which is perfectly normal in character so far as the chromosomes are concerned. Even in those cases in which the members of one chromosome pair completely fail of synapsis in the primary spermatocyte prophases and go through the first division as independent elements, there occurs a transient attachment of their two derivative chromatids in the prophase of the second division, which is sufficient to ensure the normal reduction of this pair also.

In Protortonia, with synapsis almost completely lost, we do indeed find a regulated distribution of chromosomes resulting in a normal reduction, but the mechanism which ensures this result is extremely difficult to analyse. The first division is certainly equational for three, probably for all, of the chromosomes, and the second is positively reductional for the heterochromosome, and probably for all. The five chromatids which enter the second division form short chains,—sometimes two chains of two elements each with the heterochromosome detached, sometimes one chain of two, and one of three elements with the heterochromosome occupying either the terminal or the subterminal position in the latter. The chains then become appressed, bringing the chromosomes into a single row in which only the heterochromosome may be recognized by its size. That its position in the chain, and by analogy the position of the other elements also, is not entirely a matter of chance determination is shown by the following figures. In a total of 358 cells favorable for counting, the heterochromosome was terminal in position in 74 per cent of the cases, subterminal in 23 per cent, and median in 2 per cent, instead of the 2:2:1 ratio to be expected on a purely random placement. Spindle fibers then develop at either end of the single chain of chromosomes and the chain divides transversely, in such a way that three chromosomes always pass to one pole and two to the other. The plane of division is always such as to include the heterochromosome, whatever its position in the chain, in the group of three, never in the group of two, chromosomes. Here then, we are confronted with a successfully regulated reduction without a synapsis of the chromosomes. But what factors underlie the ordered arrangement of the chromosomes which ensures this end is quite unknown.

Pseudococcus, Phenacoccus, and Gossyparia confront us with a second distinct type of reduction regulation without a preparatory synapsis of the chromosomes. In each of these forms, as remarked above, the abnormal set of chromosomes is regularly separated from the normal set in the second meiotic division. Attempting an analysis of this process, we can discern at least two factors. First, there is a marked tendency for the degenerating het-

eropycnotic chromosomes to stick together in a single mass formation; this mutual adherence may well cause them to act as a single unit and accordingly to pass together to one pole in the reduction division. In the case of Protortonia, of course, no such factor can be operative, since there a regulated reductional distribution of the chromosomes is achieved without any trace of such adherence among the chromosomes of either set,—and indeed, it may well be that the clumping of chromosomes in Gossyparia and Pseudococcus is quite secondary to the regulation of reduction.

The second factor would seem to lie in the spindle mechanism. In the Pseudococcus-Gossyparia type the chromosomes of the heteropycnotic group reach their maximum degree of condensation, and are accordingly ready for the division, long before those of the normal group, whose condensation is comparatively slow. A complete half spindle then forms in connection with the chromosomes of the heteropycnotic group, while those of the normal group are still in a relatively diffuse state. The division apparatus being thus complete for the heteropycnotic chromosomes, the division proceeds as far as they are concerned. The normal chromosomes form an inert group not yet ready for division; accordingly no spindle fibers can form in connection with them, and they are simply left behind as the heteropycnotic chromosomes move toward the one pole already formed in the cell. Of course this implies a greater lack of synchrony in the development of the two sets of chromosomes prior to the second or reductional division, than is found in the first division prophases, and cytological proof for this subsidiary hypothesis is not available. Still, since the changes which cause the degeneration of the one chromosome set are primarily changes in homology with consequent loss of synapsis, a disturbance of the reduction division is perhaps to be expected even though equational mitoses may still go on quite normally. Moreover, strong support for the general idea of the dependence of spindle formation upon chromosome condition is presented by the meiotic divisions of both Llaveia and Protortonia, for in these cases each separate chromosome, upon reaching a certain definite stage of condensation, forms its own spindle. Further evidence on the same point is offered by certain forms which have already attained the haploid condition. Thus in the primary spermatocytes of certain of the Hymenoptera (in Paracopidosomopsis, Vespa, and others) a half spindle forms in connection with the single haploid set of chromosomes just prior to the abortive cytoplasmic division. The nuclear division is suppressed entirely in these cases, but there does still occur a slight movement of the single set of chromosomes toward the single pole of the half spindle, —a movement quite comparable to that of the heteropycnotic chromosomes in the Gossyparia-Pseudococcus reduction division. In the Gossyparia-Pseudococcus cases the presence of the delayed normal group of chromosomes suffices to bring about the completed division of the nucleus. With the final loss of the heteropycnotic group and its precociously formed half spindle, either one of two possibilities might be expected. The reduction division may be omitted entirely. Or, a half spindle may form when the chromosomes of the normal group reach complete condensation, and the division itself be abortive as in the case of the wasps. As a matter of fact, in all the coccids which have become completely haploid in the male sex (Icerya, Crypticerya, and Echinicerya), all trace of a reduction division has been lost. No reduction spindle

forms; a single meiotic division demonstrably equational in character is completed; and normal haploid gametes are thus produced.

It must of course be recognized that whatever factors underlie the regulation of the reduction division in Protortonia may also be operative in Pseudococcus and Gossyparia. Thus the two factors just discussed, the adherence of the chromosomes of one set to each other, and the spindle formation, may, as was suggested earlier, be quite secondary.

All in all, although the cytological data are thus fairly complete, the factors basic to the mechanisms for the regulation of the reduction division warrant no generalization. It will be recalled that in more orthodox cases, the distribution of the members of a pair of chromosomes is assumed to rest on the process of pairing. If such pseudoreduction is requisite to the orderly distribution of a pair of chromosomes to opposite poles, then the elimination of synapsis should lead to irregularities. On this basis it is not clear why, for instance, both members of a pair of chromosomes do not occasionally proceed to the same pole. However, no such irregularities are found in the coccids; whatever the factors which replace pseudoreduction in these cases, they do result in an orderly segregation of the chromosomes. We are not prepared to analyse the relation between pseudoreduction and segregation, ordinarily assumed to be one of cause and effect; we wish only to point out that exceptions to the usual relation are not confined to the coccids. Thus many cases of m chromosomes and XY pairs of sex chromosomes attest the fact that segregation is possible without pseudoreduction. It is not unnatural to assume that in cases such as Pseudococcus similar forces controlling the distribution to opposite poles are still active, even though degenerative changes have otherwise altered one member of each chromosome pair. We are not deluding ourselves in considering that an explanation of the difficulty is thus provided, but we do submit that the question is not confined to the coccids but occurs also in instances far removed from the present ones.

Induction of parthenogenetic development in eggs

The coccids show no transitional stages in the acquisition of this third factor in our tentative analysis of the establishment of a permanent haploidy,—namely, the ability of the mature egg to develop without fertilization. The end stage, in which this ability is already established, is realized in the iceryines. The eggs of these species, whether of a virgin or fertilized female or hermaphrodite, are able to develop without fertilization and with the reduced or haploid chromosome complement. Intermediate stages in the development of such a faculty as this are, to be sure, rather difficult to visualize. One expectation, as suggested before, might take the form of a partial fertilization, in which the sperms only activate the eggs, and take no further part in their subsequent development. However, in Gossyparia, in which such a result would appear to be a very natural consequence of the degeneration of the chromosomes in one-half of the spermatids, this condition is not realized. The occasional production of aberrant sperm by the spermatids containing the abnormal chromosomes might seem to justify the suspicion that such a possible partial fertilization might now and again be realized. But the weight of cytological evidence is all against such an hypothesis,—for, in the large number of individuals studied, no actual haploid was ever encountered, nor yet any fertilized egg or embryo prior to the late blastula

stage which contained the set of degenerating chromosomes.

Again, an intermediate condition might be examplified by a normally diploid species in which some few eggs might occasionally develop independently and without fertilization. No such cases of accidental parthenogenesis have, however, been encountered in the course of the cytological work; nor have breeding experiments, quite extensive in the cases of Protortonia and Pseudococcus, ever indicated the production of offspring by a virgin female.

Finally, one might expect that, in those species close to haploidy in other respects, as for example in the chromosome conditions in the male line, the eggs would be more than ordinarily susceptible to artificial stimulation and that consequently parthenogenetic development could be induced by experimental means. To test this hypothesis various experiments have been tried with Pseudococcus (Schrader, unpublished data). The application of extreme heat and cold during the critical period in the development of the eggs has uniformly failed to induce any parthenogenetic development. Again, the males were X-rayed, in the hope of destroying the chromatin while retaining the ability of the sperm to activate the eggs, and thus inducing gynogenesis,—but always with completely negative results. It should be added, however, that not all the experiments referred to were sufficiently extensive to preclude the possibility of advance along these lines.

So far, then, as our study of the coccids has shown, the ability of the eggs to start development without fertilization or other restoration of diploidy would seem to be of an all or none character. Even those species which we regard as close to haploidy in the male line show no indication of this complementary change in the female which must of necessity occur if the haploidy is to be permanent. It is possible that the actual achievement of haploidy by the male may somehow induce parthenogenesis in the female, although we must admit that the nature of such a connection is as yet quite inexplicable. That the change in the female is not necessarily induced by the presence of but one kind of sperm, instead of two,—one conceivable way in which haploidy in the male might react upon the female—is shown in Gossyparia. That the change has occurred, within the limits of the coccid group, either with or after the establishment of male haploidy, is demonstrated by the iceryines. But we can offer no evidence as to its mode of origin or the nature of its connection, if any, with those changes in the male line which we interpret as indicative of incipient haploidy.

Sex determination

If we adhere to our plan of analysing the problem as a whole by following step by step the conditions presented by the series of coccids here under consideration, this aspect of the subject will also begin with Llaveia.

In Llaveia the process of sex determination rests on an ordinary XO — XX chromosome mechanism, the male with its five chromosomes representing the heterogametic sex and the female with six chromosomes the homogametic sex. In every way the case seems quite orthodox and there is no reason to suspect that any other than the usual type of sex determination is represented in this species

The evidence therefore strongly suggests that species with haploid males arose from species in which the ordinary mechanism obtains. Protortonia furnishes a very good first departure from the orthodox condition, but it already carries with

it certain stumbling blocks to an analysis. Superficially it is, like Llaveia, an instance of XO males and XX females. But if the present interpretation of its meiosis is correct, the chromosomes of the two types of sperm produced are not subject to random segregation. Instead, the X is always associated with two certain autosomes, all three finding homologous partners in the female pronucleus,—whereas the two autosomes in the other type of sperm are never represented in the female at all, being confined strictly to the male line.

But exactly what the bearing of this may be on the next step of the series (Pseudococcus and Phenacoccus) is not clear, for these animals have apparently lost entirely the sex chromosome mechanism represented in such a typical manner in Llaveia. But that a relationship exists between the Protortonia and Pseudococcus types is more than likely, for the outstanding feature common to both lies in the fact that they have a regulated segregation division through which one half of the autosomes is strictly confined to one type of sperm and the other half to the second type. It is unfortunate that in Pseudococcus the tracing of these two groups of chromosomes after the last spermatocyte division to and including the formation of spermatozoa presents some difficulty, for there is some evidence that in Pseudococcus the sperms which carry the heteropycnotic group of chromosomes are not always viable. If this proves to be the case, it would bridge the gap to the Phenacoccus condition, where the differential mortality in the two types of sperm seems already fully established (unpublished data, Hughes-Schrader).

Be that as it may, the relation that these two groups of chromosomes bear to sex determination is far from clear. It has been suggested independently by Gutherz ('23) and Schrader ('23) that one of the groups may represent the X and the other the Y chromosome (their nature perhaps comparable to compound sex chromosomes). It would be difficult to decide which group corresponds to the X and which to the Y, for certainly in ordinary cases the X and Y are not thus differentiated by degrees of heteropycnosis, and there is no reason to ascribe this feature specifically to either X or Y. At any rate, this interpretation does not solve the present difficulty, for two obstacles remain. First, what has occurred to alter the ordinary XO—XX mechanism of the Llaveia type to the peculiar conditions of Pseudococcus and Phenacoccus? And second, what is the mechanism which obtains when one of these two types of sperm fails to become mature or functional? Indeed in Gossyparia, where the cytology has been rather fully worked out, the latter condition is completely established, and cytologically speaking, only one of the two groups of chromosomes ever form functional sperm. Moreover, this is not the heteropycnotic group, —for that degenerates and thus demonstrates that if an X—Y chromosome analogy is resorted to, it is the Y that is represented by the precociously condensing chromosomes, and not the X.

The suggestions made in this connection by Schrader ('29) may be mentioned. According to one of these, the unpaired or heterochromosome of Llaveia and Protortonia males has been eliminated. Indeed, a hint of this may be contained in the behavior of the heterochromosome of Protortonia, which, unlike the sex chromosome of Llaveia, is lagging instead of precocious in its condensation. Maleness thereafter is the result of a partial or complete incapacitation of one complete set of the autosomes that remain.

This partial or complete incapacitation,

however, has as one of its consequences, the production of one kind of sperm only. Accepting this, as one may well do on the evidence adduced in the Gossyparia case, one is confronted with the difficulty of accounting for the production of two sexes with one type of egg and one type of sperm. Manifestly this is not possible under the ordinary conception of the sex chromosome mechanism. Despite the cytological identity of all the sperms produced, two types must be present. It was for this reason that Schrader ('29) suggested that 50 per cent of the sperms carry a gene inducing heteropycnosis in one set of autosomes and that despite cytological evidence to the contrary some crossing over occurs between the chromosomes of the heteropycnotic and those of the normal group. Thus half of the sperms containing the normal group carries the gene while the other half carries its normal allelomorph. (The same is true of the sperms containing the heteropycnotic group, which, however, have no future and need not enter into the final considerations.) Eggs fertilized by sperm carrying the gene for heteropycnosis develop into males—those fertilized by sperm with the normal gene, into females.

But even accepting this highly hypothetical elaboration we are still confronted with the difficulty of a final step. How does the Gossyparia stage reach that embodied in the iceryine coccids, where haploidy is actually established? Here the explanation no longer rests solely on the sperms, for the egg unaided produces males, while all fertilized eggs give rise to females only.

The promise of a different attack always inherent in the investigation of exceptional cases is given by the discoveries of A. R. and P. W. Whiting (Whiting, P. W. & Whiting, A. R., '25; Whiting, A. R., '27a, '27b) in Habrobracon. In exceptional cases there are produced here males which show not only maternal but also paternal characters. They therefore have come from fertilized eggs. Moreover the genetic evidence, although concededly not entirely conclusive, strongly suggests that at least some of these males are diploid. The high degree of sterility in these males suggests abnormality, but that fact by no means rules out the possibility that an elucidation of the conditions in these very males may throw much light on the processes involved in haploid parthenogenesis.

We can do no more than suggest as we have done earlier that at present only two hypotheses will take all the known facts into account.

One is that of Goldschmidt, which assumes that maleness is carried in the cytoplasm of the egg and is constant, while femaleness is carried in the chromosomes. If FF > M > F, then the presence of one set of chromosomes (as in the unfertilized egg) or two sets of chromosomes (as in the fertilized egg) will determine the sex of the developing individual. We repeat that this hypothesis should be kept in mind in all future consideration of the question. A demonstration of its correctness would imply that in the interval between the conditions in Gossyparia and those of Icerya, the main change consisted in the acquisition of the faculty of imposing the factor for maleness on the cytoplasm of the egg.

The second hypothesis is the algebraic sum hypothesis of Schrader and Sturtevant already mentioned earlier in the paper. Its departure from Bridges' interpretation lies primarily in the conception of the action of the sex determining factors. According to Bridges, sexual or any other characters are the index of a point of balance of genes concerned in their expression. As long as the proportion of the number of X chromosomes to the sets of autosomes is the same this genic balance will not be altered, and thus $X + A = 2X + 2A = 3X + 3A = 4X + 4A$ = female.

On the hypothesis of Schrader and Sturtevant the decision rests on the degree of preponderance of the genetic effect of the factors for one sex over those of the other sex. A certain degree of such preponderance is necessary before a clearcut determination of sex is possible. Thus it was suggested that on the basis of arbitrarily assigning appropriate numerical values to the X chromosome (or femaleness) and to the autosomes (or maleness), a difference of five or less brings about male development, whereas a difference of seven or greater is conducive to female development (see Table I). It will be recognized that if the X has one value and A another, the difference between them will increase as the haploid sets of chromosomes increase in number, and that thus a range from maleness to femaleness will result.

Although very close to his own general interpretation, this hypothesis is not accepted by Goldschmidt ('27, page 675). Bridges' objections, as already stated, are based mainly on the fact that the numerical differences between diploid and triploid individuals on the one hand and males and females on the other are disproportionate to the phaenotypical differences actually observed,—and furthermore that his evidence in certain mosaics of Drosophila indicates that haploid individuals of that species would indeed be female if viable. The evidence for the latter claim is, however, incomplete; and while the former seems admittedly well founded, we submit that in view of our lack of knowledge of the reactions involved no final decision is warranted. Withal it is of course possible, as Bridges himself suggests ('25), that cases such as Icerya cannot be placed upon the same basis as Drosophila.

There can be little doubt that the genic balance hypothesis is supported by a great body of evidence and that in general polyploidy does seem to induce no phaenotypic changes other than those inherent in the different cell sizes involved. On the other hand, polyploid forms have never been subjected to a complete analysis from this point of view. Thus even von Wettstein ('24), whose conclusions on this point agree with those of Bridges, mentions the fact that in one of the mosses, *Bryum caespiticum*, the experimentally produced hermaphroditic tetraploid gametophyte showed a markedly increased protandry when compared with the diploid gametophyte of the same species. Not only were the male organs older when the female organs developed, but the proportion of female to male organs was altered from 1 ♀ to 4.98 ♂ in the diploid gametophyte to 1 ♀ to 13.3 ♂ in the tetraploid. These changes are certainly not interpretable on the basis of cell size differences alone.

Again, Blakeslee and Belling ('24) state that in the shape of the capsules of diploid and tetraploid Datura plants "we seem to have a qualitative rather than a quantitative change of form."

Finally may be mentioned the recent findings of Mangelsdorf and Fraps ('31), who report that in *Zea mays* a definite quantitative relationship exists between the number of genes for yellow pigmentation (Y) and the amount of vitamin A produced in the endosperm. The presence of the allelomorphic gene y induces the production of only a negligible quantity of this enzyme (less than .05 units per gtam) whereas in the presence of one Y this quantity rises to 2.25 units per gram. However, the most striking feature so far as the present discussion is concerned lies in the fact that the number of Y genes has a direct and progressive effect on this quantity, so that 2 Y bring about the production of 5 units, and 3 Y the production of 7.5 units per gram,—the triple dose being made possible of course by the fact that

the endosperm is triploid. If now an experiment could be devised to decide whether a varying number of haploid sets (each carrying Y) produces correspondingly varying amounts of enzyme, the two hypotheses in question could be tested. Such an experiment would become possible if a tetraploid (or any polyploid higher than triploid) endosperm could be obtained, as for instance by the use of X rays or the effect of temperature changes.

The fate of the algebraic sum hypothesis thus may be finally decided if such work as that of Mangelsdorf and Fraps be pushed further in the direction indicated. So far as the hypothesis of Goldschmidt is concerned it may be pointed out that it already has received support in his own findings on Lymantria. For if, as he believes, certain factors in the Y exert an effect on the future sex determination before the egg has been fertilized such an influence must occur through the cytoplasm.

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HIBERNATION IN MAMMALS

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HIBERNATION is often referred to as "winter-sleep" in English, "*Winterschlaf*" in German and "*sommeil-hivernal*" in French. It is also called "torpor," "lethargy," and, in Italian, "*letargo*." These terms may be considered essentially synonymous. They involve an inactive state in which the metabolism is so greatly lowered that the body temperature is only a little higher than that of the surroundings. A limitation of the term hibernation to this condition and not applying it in the older more literary sense of "spending the winter" would make the meaning of the word clearer.

It should be stressed that hibernation is not ordinary sleep occurring in the winter. This was recognized long ago by Horvath (1881), who repeated a statement of the botanist, Ferd. Cohn, that "*Winterschlaf*" is not sleep and has nothing to do with winter. In this way he emphasized that hibernation may occur even in the summer and that the insensibility is far deeper than in ordinary sleep. If such a meaning can be given "*Winterschlaf*" there should be little difficulty in limiting the term "hibernation" to actual states of torpor and also in having it include all such states, not excepting those that occur in summer in the field or laboratory. There is no evidence that mammals ever become insensitive or partly torpid because of warm surroundings, all reported cases of lowered metabolism apparently having occurred when the surrounding temperature was considerably below that of the normal animal. For this reason the term "aestivation" appears inappropriate for summer torpor in mammals, although it may be proper for inactivity actually produced by surrounding high temperatures. Aestivation might be used for the denning up of the animals following a drying of the vegetation by the heat in the summer, but since any known cases of semi-torpor at this season are produced by cold such conditions should, it would seem, be called partial hibernation.

ANIMALS THAT HIBERNATE

Hibernation is common in such invertebrates as the snails in the Mollusca and the crustaceans, insects, arachnids and myriapods in the Arthropoda. It is the usual winter condition of most amphibians in colder climates and of terrestrial reptiles such as the tortoises, lizards and snakes. Invertebrates and the lower vertebrates are generally considered as having no heat-regulating mechanism, and since their temperature varies chiefly with that of the surroundings they are said to be poikilothermal or cold blooded. Recently, however, evidence has been produced that the turtle has some power to regulate the temperature of its body (Baldwin, 1925). All birds and most mammals maintain a relatively high and almost con-

stant body temperature regardless of the environment, and are said to be homoiothermal or warm blooded. Hibernating mammals do not appear to maintain a very constant temperature and at times definitely assume the poikilothermal state, so that their temperature is only a little higher than that of the surrounding atmosphere or soil.

Hibernation has been studied by various workers in monotremes, insectivores (hedgehogs), bats, and in several genera of rodents (woodchucks, dormice, ground squirrels, prairie dogs, some chipmunks and certain jumping and pocket mice). Mills (1892) says the porcupine, a large spiny rodent, hibernates but Pratt (1923) and Anthony (1928) state that this animal does not hibernate. According to Pratt (1923) and Bailey (1926) some northern species of carnivores (raccoons, skunks and badgers) hibernate. Anthony (1928) states that raccoons hibernate and skunks and badgers "den up" during very cold weather. All three of these writers state that some bears hibernate. Other workers (e.g. Merzbacher, 1904) deny that bears enter into a real state of hibernation and call attention to the fact that the young, usually two in number, are born in late winter and that the body temperature of the mother could not be low at that time. Dubois (1896) calls attention to the vapors emerging from the winter den of the bear, and he and Adler (1926) each state that bears and badgers maintain a high temperature. Seton (1928) states that the raccoon, skunk and bear are partial hibernators in the northern regions, but that they do not assume a death-like torpor.

It may be noted that the hibernating animals do not belong to any one order but that most of them live in the ground and have no access to their usual food during the time the ground is frozen. Horvath (1874, 1881) sought some test whereby one could determine whether a given species could hibernate or not. He found that animals that were known not to hibernate would die when immersed to the neck in cold water if the body temperature fell below 19°C. (essentially confirmed by Britton, 1922), whereas known hibernators would survive at body temperatures a few degrees above the freezing point of water. The latter finding was confirmed by Tait and Britton (1923), who found that a woodchuck would recover if its body was cooled even to 3°C. by the immersion method. The author has observed that ground squirrels, caught by "drowning out" methods become very torpid while wet in cold air, but recover when warmed. It seems probable that this test developed by Horvath may help in distinguishing between hibernators and non-hibernators. However, placing several animals of a species in a cold environment in the fall and winter probably would be the safer practice.

PLACE OF HIBERNATION

Barkow (1846) states that bats hibernate in stone walls, cellars, and hollow trees. Dormice hibernate in dry holes under rocks, roots or garden walls, depending on the species, and the hedgehog hibernates under roots of trees and shrubs and under garden walls. He also states that the hamster hibernates 5–10 feet and the marmot 3–7 feet underground in a nest lined with vegetation and that it closes its burrow in the winter. North American bats hibernate largely in caves (Bailey, 1924; Hahn, 1908). Ground squirrels hibernate in nests made of dry vegetation in hollowed-out underground chambers connected with their burrows. The chambers vary as to depth and size with the species. In the thirteen-lined ground squirrel, with which the author has worked, 24 nests studied varied from 4 to 10 inches in diameter and from about 3 to 27 inches below the surface (Johnson, 1917). In this and other species these nests may be connected with a drain and the entrance to the burrow is always plugged with soil before hibernation (Johnson, 1917; Shaw, 1925a). Prairie dogs hibernate in larger nests 10 or more feet below the surface (Merriam, 1901; Swenk, 1915). Their nests may be above the main tunnel as a protection against the burrow being filled with water; the entrance is not closed, possibly because the animals hibernate less than ground squirrels. Other American rodents hibernate under ground or in nests under stones. Apparently raccoons hibernate in hollow logs. If skunks and badgers hibernate they would do so in underground chambers where they normally sleep.

Food stores are sometimes found in the nests of rodents. An unusual case was observed by the author. A ground squirrel, *Citellus tridecemlineatus tridecemlineatus*, had stored about 24,000 kernels of oats

in one underground chamber and about 4,000 in another (Johnson, 1917). Oats, wheat, corn and weed seeds were frequently found in the excavations in which the hibernation nests were made, but in decreasing quantities with the advance of autumn (Johnson, 1917), suggesting that this food is eaten chiefly before entrance into hibernation. However, storage of grain was not found to be universal in this species (Johnson, 1917; Fitzpatrick, 1925). Bailey (1926) reports that there is storage of seeds and grains in the pocket mice and some of the chipmunks which are not very fat when they hibernate but apparently wake at intervals to eat.

Whether animals store food or not probably depends partly on its abundance preceding the hibernation period. While different species do not hibernate at the same time or become equally torpid, it is generally agreed by most writers that hibernation serves to conserve the life of the species that hibernate and that torpor is associated primarily with a cold season when food is impossible to secure. Whether every such species would perish if it should not be able to become torpid is difficult to determine, but this appears probable.

HIBERNATION IN THE SUMMER

That hibernation is not a condition which can occur only in the winter has been shown by a number of workers. Forel (1887) found that two dormice hibernated first in the spring after becoming fat and remained lethargic most of the summer. Horvath (1881) observed hibernation in ground squirrels in the laboratory at 22°C. Polimanti (1912) refers to summer torpor observed by Brown-Sequard in dormice lasting a week at external temperatures of 15° to 20°C., and also in marmots (European woodchucks) in June at external temperatures of 21.5° to 23°C. Bats may hibernate in June at 15°–16°C. according to Koennick (Adler, 1926). Summer torpor in thirteen-lined ground squirrels has been observed by the author to take place in a refrigerator each summer since 1924 (Johnson, 1925, 1930). In fact, hibernation was found more commonly in the summer than in the spring (Johnson, 1930). Many cases of partial hibernation have been observed in the animal house on cool mornings in August and also during later fall and winter months when the temperature fell to about 21°C. With what may be considered typical summer temperatures of about 24°C. or above no hibernation was observed. Cases of partial hibernation on cool summer days have been reported in the Townsend ground squirrel by Shaw (1925b) and in the thirteen-lined form by Wade (1930).

The tenrec of Madagascar has often been cited as an animal that hibernates in summer, but Milne-Edwards (1857) has pointed out that several workers have reported this animal hibernating during the cold season.

Since hibernation may occur in the summer in the laboratory it would be expected that it may also occur in the field, as Horvath (1881) suggested, at temperatures below 22°C. A "drowsy" Columbian ground squirrel was dug out of its burrow in August, but all efforts to find a torpid animal prior to December 13 failed (Shaw, 1925a). Seeking for this condition in the thirteen-lined ground squirrel Wade (1930) procured his earliest record of hibernation on October 16. If the animals are partly torpid in the early fall, they must be so slightly torpid that they are aroused by the sounds of the digging and are fully active when found.

Indirect evidence that such a condition may occur in nature is produced by Shaw (1925a), who found that the Columbian ground squirrels had almost all retired to their burrows by August 10 one year and in another drier summer all had disappeared by August 7 (1925c). Similar observations that hot dry weather and a consequent drying of vegetation send ground squirrels (related to our prairie dogs) of Turkestan into their burrows by June 1 is given by Kashkarov and Lein (1927). Wade (1930) mentions the disappearance of wild thirteen-lined ground squirrels one year in eastern Nebraska in hot weather early in September. He also found that of 22 animals transferred to outdoor pens in the spring nine plugged the entrance to their burrows, one in May, two in July, five in August and one in September. Wade also states that the individuals at large in the fields in late September were young or lean ones.

It has been the experience of the author that it is more difficult to secure ground squirrels from boys in western Kansas in August and September than in April to July, a fact which would support Wade's statement. However, many animals have been secured in the fall in the Dakotas, in Illinois and in Kansas, even as late as September and October.

LENGTH OF HIBERNATION

Two things make it difficult to state how long a given species hibernates. One of these is the apparent tendency of torpid mammals to wake up at intervals and the other is the possibility of some individuals of a species hibernating in the early fall when others are still at large. The waking of hibernating

mammals every few days has been observed by Barkow (1846) in ziesels or ground squirrels after one to seven days of torpor, and in hedgehogs; by Horvath (1878) in ground squirrels after torpor for four days; by Mangili (1807), Valentin (1857) and Dubois (1896) in marmots, after periods of torpor varying from a few days to three or four weeks; and by Shaw (1925a, b) in the Columbian and Townsend ground squirrels.

The author has found in many experiments, each involving 20 animals kept in the refrigerator for two weeks, that some of the animals will usually hibernate within one to three days and then awaken from one to ten days later, remaining active for a day or more. In cases where animals were in the refrigerator for long periods, castrated males were in continuous hibernation as long as 15, 16, 18 and 33 days and normal males for 13, 14 and 15 days, as judged by daily observations and their lack of feeding.

To avoid any possibility of animals waking between daily observations unbeknown to the observer, further records were taken for over four months on eight *C. t. pallidus* ground squirrels which had already been in the refrigerator 25 days. Three or four grains of oats were dropped gently on the back of the torpid animal, which would fall off only when the animal woke or moved about. The food placed in the cages consisted of dry oats and a small amount of green grass at first, but later carrots and a few kernels of oats were placed in the cages. The animals were seldom handled as previous observations had confirmed Dubois' (1896) statement that taking temperatures, etc., caused more frequent awakening. The grains of oats appeared not to stimulate waking. The range of continuous hibernation was from one to eighteen days with an average of approximately six days. One record each of 18, 17, 14 and 13 days of continuous hibernation was made, but four records of 11 days and six records of 10 days were made. There appeared to be some tendency towards a lengthening of the periods of hibernation from an average of about four at first to about eight days after a few weeks in the refrigerator. This may indicate that the torpor is more prolonged after the first few periods, although it is probably partly accounted for by the lowering of the refrigerator temperature from about 11° to about 3°C. during the course of the experiment. The average time during which the animals remained awake between periods of torpor was approximately one day. The faeces voided by each animal during the first two months of this experiment were proportional to the time spent awake. On the 62nd day of the experiment the animals were carefully transferred to clean cages and in a total of over 80 observations the animals, almost without exception, were found to void an appreciable amount of urine and faeces each time they were awake. In some cases as many as 20 or 25 faecal masses and large amounts of urine were seen. Apparently when such surprising amounts were found the animal had eaten more freely than usual. It appeared probable that most of the food passed through the animal before it became torpid again. These observations support the statements of others that these short periods of waking are caused by the stimuli produced by the urine in the bladder and faeces in the rectum.

Carrots and apples fed at different times in the experiment usually showed tooth marks after an animal had been awake for a few hours, but in several instances no food appeared to have been eaten. A few grains of oats were sometimes hulled and eaten, but most of the oats were left untouched. While the quantities of food taken at any one time were as a rule small, it should be stated that near the end of the experiment and to a less extent at other times an animal which was thin might consume large quantities of carrots in one or two days and then go back into hibernation. In general, these observations confirm those of Horvath (1878), who found that ground squirrels ate when awake more than a few hours.

It is not known whether animals wake at intervals in their burrows. One of the author's animals, which had built its nest within six inches of the surface in an outdoor cage in Chicago, came out of its burrow in late December and in late January when the weather was warm. It seems quite probable that waking occurs at intervals throughout the winter in nature, for the ground squirrels continued to do so in the refrigerator even at 2°–3°C. Waking may be more frequent in the fall because at that time the soil temperature and therefore the metabolism is higher than in mid-winter and there will be formed more urine and faeces.

Different individuals of a single species may not spend the same amount of time in hibernation. Old hedgehogs may hibernate earlier than young ones (Barkow, 1846). Old ground squirrels den up first and the females go in before the males and appear several days later in the spring (Shaw, 1925b; Wade, 1930; Johnson, unpublished data), so that the average period spent underground by the Columbian ground squirrel is 220 days in the female and 204 days in the male (Shaw, 1925b). The fact that these animals are doubtless not torpid all of this time, together with the other variations also presented, will make it clear that only approximate figures can be given for the length of hibernation in different species.

According to Barkow (1846) the hedgehog is underground four to five months, from November or December to March or April. Merzbacher (1904) gives this period as three or four months for the

hedgehog and Lapland marmot, and two or three months for German marmots, badgers, dormice and ground squirrels. Howell (1915) states that woodchucks hibernate four to six months. Raccoons hibernate nearly four months in the Red River Valley (Seton, 1928) and three to four months in Ohio (Williams, 1909). Thirteen-lined ground squirrels have been seen as late as October in Illinois (Corey, 1912; Johnson, 1917), in South Dakota (Hahn, 1914; Johnson, 1917) and in Nebraska (Wade, 1930), and on November 9 in Colorado (Burnett, 1914). They appear again in March, sometimes early (Hahn, 1914, in South Dakota) but more often late in the month (Burnett, 1914, Colorado; Corey, 1912, Illinois). In Kansas both the typical variety and the paler variety from the western part have generally been procured in fairly good numbers late in March.

POSITION IN HIBERNATION

In hibernation rodents are rolled up in their nests in the ordinary sleeping position. Striped ground squirrels sit on the posterior surface of the hind legs, the back strongly arched above, the nose tucked into the fur of the posterior part of the abdomen so that the top of the head rests partly against the pelvic girdle and partly on the bottom of the nest. The weight of the animal appears to be divided between the hind legs, the posterior dorsal part of the sacrum and the posterior dorsal part of the head. The Townsend species is illustrated in this position by Shaw (1925b), but the Columbian rests on the sacrum alone (Shaw, 1925a) as does also the *Callospermophilus* form. The fore legs are held close at the sides of the head. The eyes and mouth are tightly closed. The outside curvature of the body describes nearly a circle and it lacks only a little width in the middle to form a perfect sphere. This position doubtless tends to conserve body heat.

IMPERFECT TEMPERATURE CONTROL OF HIBERNATING MAMMALS

That the temperature of hibernating mammals, even when not torpid, may be lower than in mammals which do not hibernate was observed long ago by Saissy (1815) and others. Saissy gave records of 25°–30°R. (32.2°–37.5°C.) for woodchucks, hedgehogs, dormice and bats. Barkow (1846) observed a drop in temperature in hedgehogs and bats in ordinary sleep, in sickness and in starvation, but concluded that they are ordinarily warm blooded when awake, bats even having temperatures as high as 41.0° and 41.6°C. Dubois (1896) also found no fluctuation in the temperatures of hibernators except in the fall. According to Merzbacher (1904), Hall found a drop in temperature in a bat during its day sleep. Marked fluctuations in temperature in *Citellus tridecemlineatus tridecemlineatus* and also in *C. t. pallidus* have been observed at all times of the year (Johnson, 1928). The temperatures of ground squirrels when not in hibernation ranged from about 32° to about 41°C., but a range of 35° to 39°C. was common in a warm room and of 31° to 36°C. in a cold room. The lower normal temperatures grade into those of slight torpor at about 29°–32°C. The highest animal temperature recorded, 42.3°C., in a heated chamber was probably very close to the highest the animal can endure. The fluctuations in body temperature appear to be produced largely by changes in the surrounding temperature, but partly by the animal's activity and its rather poorly adjusted heat regulating mechanism. Vigorous exercise or confinement in a heated environment may cause a marked rise in body temperature (Johnson, 1928).

That this lack of temperature regulation and the accompanying power to hibernate is not a recent acquisition is indicated by the work of Martin (1901) on the spiny ant eater (*Aechidna*) and duckbill (*Ornithorhyncus*). These egg-laying animals are the lowest living representatives of the mammals. In *Aechidna* there was a fluctuation of 10°C. in the body temperature when the environment varied from 5° to 35°C. In *Ornithorhynchus* the temperature was low but more constant than in *Aechidna*. Martin found evidence for modification of both heat production and heat loss in *Ornithorhynchus*, and still greater heat control in marsupials.

Rectal temperature records (unpublished) taken almost daily on an adult male opossum, mostly in December, 1926, showed temperature variations in five readings ranging between 33.6° and 35.5° when taken in a room of between 25° and 29°C. The same animal removed to a refrigerator temperature of 4° to 6°C. showed a range of temperature varying from 33.5° to 34.7°C. A young opossum in a room temperature of 14° to 19°C. in February, 1925, showed a range of rectal temperature varying from 33.2° to 35.0°C. Two other opossums under the same conditions gave single temperature readings of 36.0°C. No hibernation was observed in four opossums in a cool cave nor in one kept at about 5°C. in a refrigerator.

Four pocket gophers (*Geomys bursarius*) kept in a cold room of about 4°C. for five days showed only slight temperature fluctuation, in one case 33.8° to 35.2°C. and in another case 35.2° to 35.8°C. The four died in a few days and like others kept in the refrigerator at other times never hibernated. A dying animal showed a rise of body temperature from 19.5° to 23.0°C. with a rise in heart beat from 40 to 124, on

removal to a warm room. As the animal died this was probably only a temporary rise in metabolism produced by the warming of the animal, and the lowered temperature cannot be considered hibernation.

Since prairie dogs (*Cynomys ludovicianus*) have been reported to hibernate only for short periods in nature it was felt that a study of their temperatures would be interesting. Forty-six daily records on seven animals in the cold room ranged chiefly between 32° and 36°C., whereas 57 daily records on five animals in the warm room showed a relatively stable temperature at 36°–37°C. (Table 1).

Three prairie dogs in a refrigerator had temperatures of 27°, 28° and 28°C. and were therefore on the verge of torpidity. Among several prairie dogs kept in a refrigerator temperature of about 5°–12°C. for several weeks at a time only three cases of normal hibernation were observed. These animals were not completely torpid, but could move very stiffly and trembled like ground squirrels in the later stages of a disturbed awaking from hibernation. The rectal temperature of one was 21.5°C. at a room temperature of 9.5°C. The second had a rectal temperature of 19.4° in a room of 9.5°C. A third was found, partly torpid, at a room temperature of 4.4°C. In breathing it made a wheezing noise, but this stopped as it gradually recovered its normal temperature. A fourth animal was considered as in abnormal hibernation. It was partly torpid at 22.0°C. cheek pouch and rectal temperatures. This animal seemed to have much difficulty in breathing, and in the quarter hour it was observed its temperature fluctuated a little with exertions but showed no real rise. The next day, however, it had a rectal temperature of 30.0°C. and was more active, although somewhat sluggish. Again 13 days later this animal was slightly torpid at rectal and pouch temperatures of 29.5° and 29.3°C. respectively. At this time it had difficulty getting air and its heart beat was somewhat irregular, showing pauses between a series of regular beats.

TABLE 1

Temperatures of Normal Prairie Dogs

	ANIMAL TEMPERATURES						
	31*	32	33	34	35	36	37
Number of records at refrigerator temperature 3°–10°C.....	1	5	8	9	7	14	2
Number of records in warm room, range about 22°–29°C.....	0	0	0	2	7	31	17

* Each degree given includes the decimals of that degree, thus 31 = 31.0° — 31.9°C.

Incidentally, from these temperature studies it may be concluded that the opossum may possibly hibernate to a slight extent, that the pocket gopher does not hibernate, and that the prairie dog hibernates only for short periods in the coldest weather. In this connection also, it is of interest to note that young mice and rats do not regulate their own temperatures well until they are ten days old (Pembrey, 1895), and even a group of adults may have a range of 1.0° to 2.0°C. (Sumner, 1913). According to Bierens de Haan (1922) a rise of 5.0°C. in external temperature produced an average rise of 0.70°C. in the body temperature of 3½ week old rats.

TEMPERATURE IN HIBERNATION

Body temperatures lower than or equal to those of the surroundings have been reported in torpid bats by Hall (1832), in marmots by Valentin, according to Barkow (1846), and by Monti and Monti (1900). In torpid ground squirrels Horvath (1872a) reported a body temperature of 2°C. in a room of 2°C., (1878) of 11.8°C. in a room of 13°C., of 11.5°C. in a room of 12°C., and of 4.6°C. in a room of 5.8°C. Barkow (1846) made similar findings but like Valentin considers that body temperatures are usually a little higher than those of the surroundings. Saissy (1815) and others found the temperatures of torpid marmots, hedgehogs, dormice and bats to be higher than those of the room, the difference being 1° to 2°C. (Quincke, 1881), i.e., 0.5° to 0.8°C. in bats in a cave of 6.4° to 7.7°C. (Delsaux, 1887); 0.25° to 2.0°C. in bats (Pembrey and White, 1896); a few tenths of a degree in the marmot (Dubois, 1896); and 1.1° in ground squirrels in a box of 2.2°C. (Shaw, 1925b).

That serious errors could be made in the study of animal temperatures in relation to room temperatures became evident to the writer in the progress of his work. The causes of these errors were eliminated by meeting the following conditions: constant room temperature, room temperature taken at the level of and near the animal, animal not in contact with a floor that was colder or warmer than rest of room, complete corrections applied to thermometers, animal and room temperatures taken immediately upon entering the room, animals disturbed as little as possible, light not used intermittently, and quietness in the hibernating room.

In a cold room (Johnson, 1928) when the temperature had become fairly constant after a gradual fall, three temperature curves of *C. t. pallidus* ground squirrels remained about 0.5° to 1.0°C. higher than the room temperature curves in three animals. Thermo-

couples placed in the bottoms of thick corkboard nests indicated body temperatures of a little less than 1.0°C. (0.5° to 1.2°C. in 92 per cent of 144 records) above that of the surroundings in ground squirrels long in deep hibernation. Of 25 records obtained by removing torpid ground squirrels from a refrigerator and immediately taking their pouch temperatures thermoelectrically, 40 per cent were less than 1.0° higher, 68 per cent were less than 2.0° higher and all the records were less than 4.0° higher than the refrigerator temperature, which ranged from 4.9° to 8.4°C. Torpid ground squirrels appear, then, to be usually about 1.0° to 3.0°C. warmer than their surroundings, but they are often less than 1.0°C. above, and may be rarely only 0.3°C. above the surrounding temperature. That Horvath and Monti and Monti and some other workers failed to observe proper precautions seems evident. The metabolism of the animal is sufficient to keep its temperature slightly above a constant surrounding temperature.

The lowest temperature in a torpid woodchuck observed by Dubois was 4.6°C. He states that the temperature of bats may fall to 5.0°C. or even to 1.2°C. in hibernation. Horvath (1872a) gives the lower temperatures of hibernating ziesels as 2.0° and later (1881) as varying between 1.8° and −0.2°C. The animal with a temperature of −0.2°C. woke up as a result of an external temperature of −0.5°C. As has already been pointed out, some of Horvath's temperatures were possibly not reliable; hence these may not be either. The lowest temperature given by Horvath was recorded during a falling outside temperature and may have been taken near the surface of the body; the emergent stem may have slightly lowered the reading, or the thermometer may not have been accurate. Dubois (1896) states that Brehm found temperatures of bats as low as 1.2°C. Adler (1926) states that if bats are cooled carefully and are not disturbed by touching or noise, their temperature may be lowered to 0.5°C., but that this temperature usually starts the awakening process.

That animals in hibernation may approach the freezing point of water was evidenced in my work (Johnson, 1928) in which a *C. t. tridecemlineatus* was observed with a food pouch temperature of 2.0°C. in a room of 1.0°C. This animal woke in a normal manner. That death results somewhere between 2.0° and 0.0°C. was indicated by the fact that one *C. t. pallidus*, which was almost dead, had a temperature of 0.2°C. (Johnson, 1928). It did not respire for an hour and had a very slow and abnormal awakening. An animal with a temperature of 0.0°C. breathed very slightly after 22 minutes but did not wake up. In several instances where the refrigerator temperature fell to 0.0° or slightly below, the torpid ground squirrels died. Semper (1881) reviews some reported cases of survival of frogs and other animals when frozen, but concludes that there is insufficient evidence especially that the tissues, blood, etc., were actually frozen even though the external temperature may have been much below freezing.

The death of torpid animals at freezing temperatures in this and other laboratories (e.g., Hunter, 1837) casts doubts upon the conclusions of Barkow (1846), Valentin (1857), Horvath (1881), Dubois (1896) and others that such temperatures always produce waking of a torpid mammal. Experiments have been reported (Johnson, 1929b) which showed that a lowering of the external temperature from about 3° or 4°C., to 1°C., woke some of the ground squirrels (*C. t. pallidus*) but not all, and those which woke usually went back into normal hibernation with the air temperature at 1.0°C. These animals were observed frequently, so it was not possible that any woke and went back into hibernation without being observed. Wade (1930) found that a rapid drop in room temperature to −1.0° or −2.2°C. woke most but not all his ground squirrels, some dying without awakening.

RESPIRATION IN NORMAL ANIMALS

Saissy (1815) reported respiration rates of 30, 16, 45 and 7 respectively per minute for the marmot, hedgehog, dormouse and bat at 16°R. (20°C.) in August. Barkow (1846) counted 20 to 40 respirations in sleeping hedgehogs. A surprising range has been found in ground squirrels (Johnson, 1928). Among 48 *C. t. tridecemlineatus*, there was a range of 45 to 340 inspirations a minute, with an average of 187. In 37 awake and quiet *C. t. pallidus*, respiration varied from 20 to 360, with an average of 126 a minute, while a group of 12 others, after moving or feeding averaged 213 a minute, individuals varying from 140 to 320. A rate of 100 to 200 has been considered as most common in either variety of ground squirrel. Hoy's (1875) rate of 50 a minute for ground squirrels was probably from an inactive or semi-sleeping animal, since my observations on sleeping animals gave a range of 7 to 68, with an average of about 25 a minute in the two varieties of squirrels. In addition to degree of excitation, the variation in respiration rate in ground squirrels may be largely accounted for by the existence of a slow type of inspiration, involving a great but slow expansion of the whole thorax when the animal is quiet, and of a rapid shallow expansion of the abdomen and posterior thorax seen when the animal is excited or very active.

RESPIRATION IN HIBERNATION

Mangili (1807) found respiration to be very irregular in hibernation. He reported a 15 minute pause in the respiration of the hedgehog followed by 30 to 35 slow respirations. In dormice at 1°C. he recorded 147 inspirations in 42 minutes but with pauses of 3 to 8 minutes. In other series of records the pauses ranged between 2 and 13 minutes and between 3 and 5.5 minutes.

Some correlation between temperature and frequency of respiration in hibernation was seen by Saissy (1815). In hibernation that he considered was not very deep the respiration counts per minute were 7–8 for the marmot, 4–5 for the hedgehog, 9–10 for the dormouse, and either 0 or 4–5 for the bat. In deep hibernation he saw no breathing in the bat and considered this to be the general rule with other animals in deep hibernation. Hall (1832) and Delsaux (1887) observed no respiration in very torpid bats but the latter found that they gave off 394–615 mgm. CO_2 per kgm. per hour. It must be admitted there is a greater possibility of absorption of oxygen through the thin skin of the wings of a bat than through the skin of other mammals. Ziesels at 2.5°C. body temperature and undisturbed torpid hedgehogs had no visible respiration according to Barkow (1846). Dubois (1896) observed 1–4 very feeble respiratory movements a minute in profoundly torpid marmots.

While pauses in respiration have been noted in torpid ground squirrels, absence of respiration for several minutes is probably abnormal (Johnson, 1928), for two animals that showed no respiration until 14 and 25 minutes respectively after removal to a warm room died after a slight breathing for a few minutes. Two others which respired only after 19 and 22 minutes recovered abnormally. A fifth, which showed no respiration for an hour, recovered very slowly with the aid of artificial respiration. From careful observations, it was concluded that in deeply torpid ground squirrels in a room below 10°C., inspirations may average from one-half to four a minute normally, but that they may fall somewhat lower in thin animals long in hibernation.

To determine the ability of poikilothermal mammals to endure the lack of air while in the active state Carlisle (1805) kept a hedgehog under water of 8.8°C. for 30 minutes, but apparently the animal had its nose to the surface a number of times. It recovered in two hours, whereas another kept under water of 34.4°C. died in 10 minutes, due possibly to the higher rate of metabolism when warmer. Barkow (1846) states that the normal hedgehog may sometimes endure total immersion for eight minutes, but others died in 3, 4 and 5 minutes. Hall (1832) also states that normal bats and hedgehogs drown in about 3 minutes, but two torpid bats were under water 11 and 16 minutes and a hedgehog 22.5 minutes without injury. Poisonous gases did not injure torpid bats and marmots according to Spallanzani (1803) and a hedgehog could endure nitrogen gas for 15 minutes, whereas the mouse, rat and sparrow died respectively in 2.5, 2.5 and 0.5 minutes (Saissy, 1811). Saissy also found that a hibernating animal could use up all the oxygen in a closed chamber before suffocating, whereas the rabbit absorbs only 75 per cent, the rat only 62.5 per cent, the sparrow only 42.5 per cent before dying. Delsaux (1887) showed that normal bats placed in a chamber in which the air was rarified by means of a vacuum pump to 50 mm. of mercury appeared asphyxiated, but could remain in this condition for half an hour and still recover when removed.

Delsaux (1887) reported Regnault and Reiset as finding that a marmot used only one-thirtieth as much oxygen when torpid as when awake. According to Dubois (1896) Valentin reported that a torpid animal used one-forty-first as much oxygen and eliminated one-seventy-fifth as much carbon dioxide as a normal animal. Pembrey (1903) found that the relation of the carbon dioxide excreted in hibernation (body temperature 12° to 16°C.) and in activity was about 1:100 in the dormouse and 1:10 or 1:20 in the hedgehog. Gorer (1930) points out that the highest metabolic rates of hibernating mammals were reported by Pembrey for the dormouse, about 300 cc. oxygen per kgm. per hour being absorbed when torpid at 10°C. as compared to about 8,000 cc., about 27 times as much, when awake. For the marmot the amounts were about 35 and 550 cc., about 1:16 at 10°C. and awake, respectively. Stockard (1930) gives the carbon dioxide output of a white tailed prairie dog (*Cynomys leucurus*), in hibernation November 15 at a body temperature of about 21°C., as less than one-eighth that of the same animal two and three days later when sleeping or awake but quiet at a body temperature of about 32°C. (The date and temperatures have been kindly provided by Mr. Stockard in a letter to the author.)

In studying the effect of hibernation upon the respiratory quotient $\left(\frac{CO_2}{O_2}\right)$ Dubois (1896) found that more O_2 was absorbed than was represented in the CO_2 given off and the respiratory quotient approached 0.5, and he states that Regnault and Reiset found it to be as low as 0.4, whereas in the animal awake or in the process of waking it approached unity and even exceeded unity at the very beginning of waking. Pembrey (1903) found a respiratory quotient as low as 0.23 and 0.50 in torpid dormice and hedgehogs, re-

spectively. According to Gorer (1930) several workers object to low quotients, but he concludes that the real quotient must be below 0.7 and believes that it ranges from 0.3 to 0.5. A low respiratory quotient according to Pembrey (1903) and Bayliss (1918, p. 278) indicates that there is a conversion of fat, which contains a small amount of oxygen, into carbohydrate, which contains more oxygen. Gorer (1930) considers the significance of the respiratory quotient at some length but concludes that direct evidence on the metabolism is needed and would help to determine the quotient.

HEART BEAT IN THE NORMAL AND HIBERNATING STATES

In active bats a pulse rate of 200 a minute was reported by Prunelle (Barkow, 1846). Rates of 90 a minute in a room of 19°C. and of 30 a minute just before hibernating in a room of 6°C. were found by Saissy (1815), and of 28 a minute in hibernation by Hall (1832).

In active dormice Reeve (1809) states that the rate is too rapid to count but falls to 88 a minute in beginning torpor, or to 105 at 19°C. and 88 a minute at 6°C. (Saissy, 1815). In deep torpor it falls to 16–20 (Reeve, 1809), 20–25 (Saissy, 1815), or 10–12 a minute (Spallanzani, by Barkow, 1846).

In hamsters pulsation rates of 150–200 (Sulzer, by Barkow, 1846) in activity or of 100–150 when irritated (Reeve, 1809), fall to about 60 before hibernation and as low as 12–15 in deep torpor (Reeve, 1809; Sulzer, by Barkow, 1846; Dubois, 1896).

Hedgehogs may have a pulse rate of 75 a minute in a room of 19°C., falling to 25 at 6°C. At these temperatures a marmot had 90 and 70 beats a minute respectively (Saissy, 1815). In torpor the marmot was found to have a pulse rate of 27–28 a minute (Mangili, 1807), but this rate may have been raised by the decapitation and opening of the thorax, for Saissy (1815) gives a rate of 10–12, and Dubois (1896) has made some cardiograms with a rate as low as 3–4 a minute in torpid marmots.

From the slight bleeding when a vessel was cut and from the lack of enlargement when vessels were tied in the neck and legs, Saissy (1815) concluded that there was no peripheral circulation in deep hibernation, but merely a slight ebb and flow in the vessels near the heart. He was supported in this by Brown (1847), who also agreed with Mangili (1807) that little blood reached the brain in torpor. Dubois (1896) maintained that a very slow circulation is present in hibernation, a view shared by the present writer.

Instances of heart-block, or the independent beating of auricles and ventricles, have been cited by Buchanan (1911) as occurring in the partly torpid dormouse. A complete missing of beats of the heart has been shown in an electro-cardiogram from a ground squirrel which had begun to awake from hibernation (Johnson, 1929b).

The rate of heart beat in normal ground squirrels varies greatly (Johnson, 1928). In both varieties the range was found to be about 100 to 200 in animals just awakened from normal sleep, but rose to 200 to 350 in animals held, some quiet and some struggling. In excited struggling animals the rate often rose above 350, rates of approximately 400 being sometimes recorded by counting the beats in an abbreviated manner with a stethoscope. That the rate may go still higher is shown in Figure 1a, an electro-cardiogram of a *C. t. pallidus* ground squirrel biting and struggling violently while it was held showing 8.43 beats in one second or 506 beats a minute. This is 100 times as fast as the lowest rate (5 a minute) recorded in two very torpid animals (a cardiogram of 5.53 beats a minute is shown in Figure 1b). It is 29 times faster than the average (17.4 beats) of the 22 lowest records of animals whose temperatures were below 10°C.

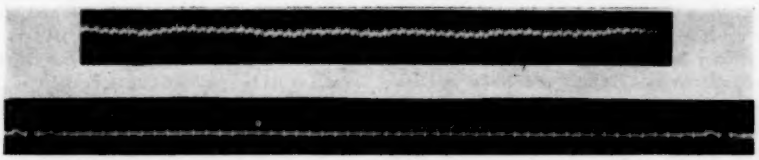

FIG. 1, A. ELECTROCARDIOGRAM OF CITELLUS TRIDECEMLINEATUS PALLIDUS, NO. 947, STRUGGLING AND BITING, SHOWING 506 BEATS A MINUTE. LEAD 1, TWO ARMS. B. ELECTROCARDIOGRAM OF C. T. PALLIDUS, NO. 938, IN DEEP HIBERNATION, SHOWING 1 BEAT IN 10.32 SECONDS OR 5.53 BEATS A MINUTE. LEAD 1, TWO ARMS. TIME 3:03.

SURVIVAL OF THE HEART

Several workers have observed the persistence of reflexes in decapitated hibernating mammals (Merzbacher, 1904) and the continued beating of the heart three hours after decapitation in a torpid marmot

(Mangili, 1807). A ground squirrel, *C. t. tridecemlineatus*, was dug out of its underground nest in the winter by the author and its heart beat observed within 8 minutes by cutting open the thorax ventrally. The heart beat was 13.5 a minute at first, the body temperature, 2.0°C., respiration rate, 2 a minute, and air temperature, 4.0°C. After 18 minutes the heart beat rate was 14 and the animal was taken into an air temperature of 0.0°C. After 47 minutes the heart beat had fallen to 6.5, with a body temperature of 5.5°C. and attempted respirations of 2.4 a minute. From 1:52 to 6:00 (taking the beginning of the experiment as 0:00 hour) the heart beat was irregular at about 2 to 4 a minute and attempted respiration stopped before 3:38. When removed to a temperature of 18°C. at 6:28 its heart beat rose to 9.2, 18 and 28 respectively at 6:38, 6:56 and 7:05. It was necessary to leave the laboratory, so the animal was then skinned. By 7:21 its heart beat rose to 61 a minute. The body was placed in 10 per cent formalin. The heart stopped beating in 30 minutes, which was seven and one-half hours after it was exposed. Another torpid ground squirrel, a *C. t. pallidus*, had a heart beat of 17 a minute when cut open, but this decreased to 6 in one hour and to 3 in two hours and ten minutes. At first the attempts at respiration were deep and frequent; the last slow and feeble attempts were noted one hour and 24 minutes after opening the thorax. The heart ceased beating sometime between two hours and ten minutes and four hours and 31 minutes after exposure. A second torpid *C. t. pallidus*, with a heart beat of 15 a minute when the thorax was cut open, showed great efforts to expand the thorax and the heart beat increased to 17 in 7 minutes, but by 23 minutes the expansion of the thorax was slight and the heart beat 10 a minute. The heart beat fell to 7 in one hour, 6 in 2 hours, 3 in 5.5 hours and stopped before 8 hours. In the last two experiments the room temperature averaged about 4°C.

The beating of the heart of the torpid animal several minutes after isolation and placing in warm Ringer's or salt solution has also been confirmed by the author. Merzbacher (1904) states that the heart of a hibernating mammal will beat for hours if excised and kept cold and moist.

Death in hibernation appears to be produced by cessation of respiration rather than of heart beat, for the heart was still beating in five ground squirrels in which no respiration was seen for respectively 14, 19, 22, 25 and 60 minutes after the animals had been removed from the cold to a warm room. The first and fourth of these died after respiring slightly for a few minutes. The others recovered very slowly, were very weak and the last one would probably have died if artificial respiration had not been resorted to (Johnson, 1928).

RESISTANCE OF TORPID MAMMALS TO TOXIC SUBSTANCES

Injected poisons produced little or no effect on torpid animals (Merzbacher, 1904). Hibernating bats were found resistant to pilocarpin, apomorphine and strychnine by Koennick, according to Adler (1926), who compares this resistance when the animal is not awakened to that of cold blooded animals. Blanchard (1903) found that torpid marmots were sensitive to inoculations of trypanosomes and to toxins of tetanus and diphtheria as well as to venom of the cobra. Hibernation merely slowed up the action of the toxins, for they were nearly as deadly to the torpid as to the normal animals.

IRRITABILITY IN HIBERNATION

While the nervous system of a torpid mammal functions to maintain a low rate of heart beat and of respiration, it becomes progressively less sensitive to stimuli as its temperature falls. Before this falls to about 30°C. thirteen-lined ground squirrels can move and respond to stimuli in practically the normal way. When it has fallen to about 20–30°C. they may move forward in a dazed manner or merely raise up stiffly and try sluggishly to bite when touched. At about 10°–15°C. the animals are more inert and are likely only to raise the head slightly or give other weak responses. If the body temperature falls to about 2°–5°C. there is usually no response even to strong mechanical stimuli such as inserting a thermometer bulb into its food pouch or pricking the animal with a needle. At low body temperatures Franklin, Richardson and *Callospermophilus* ground squirrels have been observed by the author to be as unresponsive as the thirteen-lined species. Hatt (1927) made similar observations on the *Callospermophilus* and Shaw (1925c) on the Columbian ground squirrels. Touching a torpid hedgehog caused it to breathe eight to twenty times, the respirations gradually becoming shorter and slower and the animal did not wake unless the stimulation was continued or the animal taken to a warm room.

While the immediate responses may not be made to such severe stimuli as falling from a table and breaking a collar bone or by having the nose cut open to expose nerves and blood vessels as in a young marmot (Valentin, 1857), stimuli of this strength would invariably wake a ground squirrel in due course of time. However, it is often possible to gently lift a deeply torpid ground squirrel out of the nest and

carefully insert a thermocouple into its food pouch without causing it to wake (Johnson, 1928).

Horvath (1881) states that conditions in hibernation may vary somewhat in different groups of mammals. In *Myoxus dryas* he found that the eyes were not closed as in ground squirrels, and the hamster might give forth loud cries, or more probably, draw in deep sonorous inspirations when disturbed as stated by Cleghorn (1910). The degree of immobility in bats may vary with the temperature, time of year and the species according to Dubois (1896) and others. Black tailed prairie dogs and a pocket mouse in partial hibernation with a body temperature somewhat above 20°C. were observed by the author to straighten out and make feeble attempts to crawl when held in the hand. If the temperature in these two forms can fall to 2°–5°C. it is probable they would be as inert as ground squirrels.

Electrical stimuli produced no effect on woodchucks and hedgehogs but caused slight movement on the part of dormice and bats (Saissy, 1815). Marmots were not roused by an electric spark and they were excited only for a short time by a shock from a Leyden jar according to Reeve (1809) and earlier workers quoted by him. If the electrodes were placed directly on the exposed muscles or nerves that go to them, Horvath (1872b) found that the cold muscles responded even to weak induction stimuli. Electrical stimulation of the exposed cerebral hemispheres of torpid bats produced no effect on one bat, but on another strong stimulation (coil at 6 cm.) caused inhibition of respiration for ten minutes (Merzbacher, 1903a). By stimulation of torpid ground squirrels by means of shocks from an induction coil (Harvard inductorium) the author has produced movements, such as raising of the body or even the turning of the head, which had not been produced by mechanical stimuli at the same temperature.

While considerable variation has been seen both in the tendency to hibernate and in the irritability in hibernation among large numbers of the same species of ground squirrels observed, it nevertheless appears that there is a marked general relation between body temperature and activity. This is especially evident in the regaining of powers of motion as a torpid animal wakes, observed by many authors. Britton (1922) has shown that even in a cat cooled to the point of lethargy the muscular activities return in a certain order and at somewhat definite body temperatures as the animal recovers, although such non-hibernating animals lose their power to respond to stimuli at a higher body temperature when that is lowered artificially. The production of immobility, whenever an animal's body temperature falls, suggests that the bear and possibly the raccoon do not actually become torpid, for Dubois (1896) and Bailey (1926) state that they are easily aroused, which could hardly be the case if the body temperature is very low.

EFFECT OF HIBERNATION ON WEIGHT

All workers have recognized that loss of weight in hibernation is small as compared to that in starvation and have pointed to this conserving action of lethargy as its chief function. While it is also generally recognized that there is a considerable loss in body weight in an extended period of hibernation, there is no marked agreement as to the exact loss. Bailey (1926) believed there was "only slight loss of fatty tissues." He considered the lack of food after waking and during the breeding season as drawing heavily upon the stored fat. In pocket mice and some chipmunks he observed no accumulation of fat but called attention to their stores of seeds and grains which he believed they consume at intervals of awakening. Earlier workers have generally considered that animals are fat in the fall and wake up lean in the spring, as reported for the dormouse by Murray (1826) and several others.

Marmots lost one-fourth to one-sixth of their body weight in about 130–150 days of hibernation and in two animals even in 56 and 59 days respectively, and two hedgehogs lost one-fourth of their weight in 26 and 50 days respectively (Valentin, 1857). Wade (1930) has estimated that one-half of the weight may be lost by ground squirrels which den up in late summer, and some of his records (p. 173) show losses of 59 and 61 per cent in 207 and 228 days in which the animals' burrows were closed.

The weight losses of five *C. t. tridecemlineatus* which hibernated outdoors have been studied by the author. Estimating that they changed little in weight in the four to six weeks before hibernating (they were fed well, but they also exercised considerably in digging burrows and building nests) the losses from the time of closing their burrows till they were dug out in the torpid state were: 19 per cent in 65 days; 21 per cent in 83 days; 18 per cent in 106 days; 32 and 39 per cent in 100 days. A *C. t. pallidus* lost 38 per cent in 79 days. As none of these animals hibernated as long as animals would in nature, this average loss of 28 per cent is probably lower than occurs in nature. The average daily loss was 0.32 per cent. A comparison of average weight (93 grams) of 120 *C. t. pallidus* received early in the spring with that (157 grams) of 45 adult laboratory animals which were not excessively fat in the fall would indicate an average loss of about 41 per cent from fall to spring (Johnson, 1928).

Ground squirrels which refused to hibernate when placed in a refrigerator showed marked losses if fed sparingly, but lost less or even gained slightly when fed well (Johnson, 1928). Where two or more weight records were obtained within a period of hibernation in which waking was believed not to occur, the average daily loss in eight records of 14 to 17 days was 0.57 per cent. If the loss were computed on this basis, calculating it on the reduced weight each 15 days, the animal would lose 45 per cent of its original weight in 100 days, and 59 per cent of its original weight in 150 days. Five other animals whose periods of hibernation averaged 28 days lost 0.43 per cent daily. If the successive reductions in weight are used and the losses computed in periods of 25 days each, an animal in 100 days of hibernation would lose 36 per cent, and in 150 days, 49 per cent of its original weight.

Seven *C. t. pallidus* ground squirrels were placed in a refrigerator August 5 and removed January 8, 156 days later. They were in hibernation an average of 83 per cent of this time. Five of these animals which were in good condition, weighing 147–185 gm., when placed in the refrigerator, were taken out somewhat thin, having lost 37 to 49 per cent (average 45 per cent) in weight. Two which had been very fat lost respectively 40 and 39 per cent of their original weights of 226 and 250 gm., but were still somewhat fat. Considering that the loss in hibernation in a closed underground burrow may be less than in a refrigerator, the data presented would appear to indicate that ground squirrels commonly lose 30 to 45 per cent of their weight in five months of hibernation in nature.

The loss in weight during hibernation is accounted for chiefly by the using up of the thick layers of fat under the skin, in the mesenteries, and in the mesovaria or mesorchia. In the fall the latter may be 4 mm. in thickness, their appearance suggesting thick pieces of bed quilts, but in the spring the fat may be reduced to streaks along the blood vessels which course through the epithelium to the reproductive organs (Johnson, 1928). Williams (1909) has called attention to the localization of "a heavy fat blanket" on the more exposed hind quarters and back in the hibernating raccoon. He found more than one-fourth of the body weight to be fat.

Slight temporary increases in weight have been reported by Horvath (1878), Dubois, (1896) and others, but this condition was attributed by Valentin (1857) to absorption of moisture by the fur rather than to fixation of oxygen with retention of carbon dioxide as mentioned by Pembrey and White (1896) and others. Valentin (1857) also discovered gains in weight in animals that had awakened between weighings.

THE PROCESS OF WAKING FROM HIBERNATION

Types of awaking

Two types of awakening from hibernation have been described (Johnson, 1929a): (a) A relatively rapid awakening accompanied by trembling and shaking of the head and shoulders, following a disturbing of the animal by removing it from the nest and laying it on the side or back, and either taking it to a warm room or leaving it in the cold room; (b) A more gradual awakening, usually without trembling or shaking, after removal without disturbance to a warm room, or following some handling at first after which it was placed back in the rolled up position in the nest and left in the cold room.

In the first type of awakening the breathing increased in rate, the body showed some movement of forefeet or head or of both, then more marked movements such as trembling, shivering, shaking the head sideways or jerking it up and down. These movements were accompanied by a gradual straightening of the body from the rolled up position and were

usually followed by deep, rapid and convulsive respirations, and later by the raising of the head, the getting up on the forefeet, and still later by standing on all fours. Before or at this time they became very irritable and could fight in a drunken but determined manner. Soon the eyes would open and if disturbed they would move forward, awkwardly for a few minutes. If the animal was transferred to a warm room in addition to being stimulated by being laid on its side and having its temperature taken, the steps mentioned were crowded together and the stages given might occur two at a time. This type of waking has been described in various forms by Pembrey and Pitts (1899), Hahn (1914), Dubois (1896), Shaw (1925b), Hatt (1927) and others. Merzbacher (1903) has described four stages in the return of activity in a bat waking from hibernation. These were: (1) rigidity, with only reflexes of the spinal cord; (2) hanging on, with reflexes of the medulla oblongata; (3) beginning of cerebral activity with loss of sub-cortical reflexes and accompanied by the opening of the eyes; (4) fully awake, with cortical control of sub-cortical reflexes.

In the second or relatively undisturbed type of awakening there was much abbreviation and elimination of the steps given for the first type. Increased respiration or a raising or humping of the rolled up body was often followed by a working out of the head from underneath, then by raising the head and opening the eyes accompanied by standing on the forefeet. While this type of awakening is probably typical of that in nature, the disturbed type has been the one usually described.

The opening of the eyes occurred usually in the disturbed awakening between 20° and 34°C. in 12 *C. t. pallidus* and 15 *C. t. tridecemlineatus*, and in the undisturbed type it occurred between 21° and 37°C. in 45 *C. t. pallidus*. The difference in temperature at waking therefore was not great. However, the 27 disturbed animals woke in 63 minutes on the average, whereas the undisturbed animals woke in an average of 114 minutes.

Effect of stimulation during waking

While strong stimulation at first is almost certain to produce complete awakening even in the cold, showing that irritability is not completely lost in deep torpor, even if no quick response is seen, it is interesting to note that continued stimulation during the waking by dropping small weights on the animal or by applying electrical shocks with an inductorium did not hasten the process very much and sometimes caused inhibition of the heart beat and respiration for a short time.

Mid-brain necessary for waking

Dubois (1896) found that destruction of the cerebrum and corpora quadrigemina did not prevent waking from hibernation, but a destruction of the mid-brain prevented waking. With only the medulla oblongata left the torpid marmot would live 8 to 9 hours or more but could not awake automatically and died while torpid.

The rise in respiration, heart beat and temperature

When waking from hibernation is started by some external stimulus the heart beat seems usually to take a slight lead over respiration in producing a warming of the animal (Johnson, 1929b). Figure 2 illustrates the increases in respiration, heart beat and temperature in disturbed waking in a cold room (Ia, IIa, IIIa), in a moderately warm room (Ib, IIb, IIIb), and in an unusually warm room (Ic, IIc, IIIc). It is seen that the rise in metabolism is slow at first in the cold room (a) but speeds up considerably at about 60 minutes. In the moderately

warm room (b) the rate is rather steady throughout, the respiration and heart beat showing a very great increase after 35 or 40 minutes. In the warmest room (c) the temperature rise is very pronounced as soon as the animal is removed from the cold to the warm room, indicated by the animal is fully awake, as was stated by Dubois (1896). In about 35 minutes after the animals, I, J, K and L, were taken to the very warm room (Ic) the respiration rate rose from about 8 a minute to about 150, the heart beat rose from 28 to 375 a minute, and the food pouch temperature

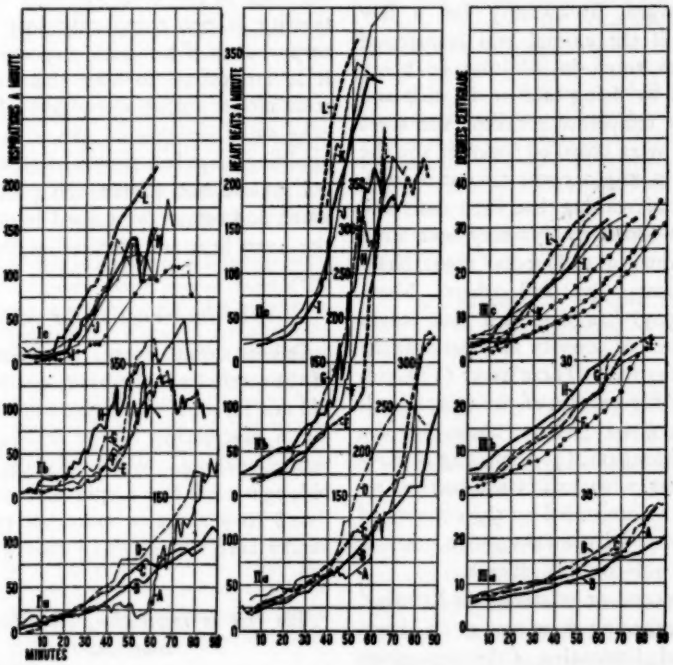

FIG. 2. GRAPHS OF INCREASE IN RESPIRATION (I), IN HEART BEAT (II) AND IN TEMPERATURE (III), IN A COLD ROOM OF ABOUT 2° TO 10°C. (a), IN A ROOM OF ABOUT 15° TO 22°C. (b), IN A WARM ROOM OF ABOUT 25° TO 35°C. (c)

The curves belonging to one animal are designated by the same capital letter, thus I a A, II a A and III a A represent the respiration, heart beat and temperature increases respectively in one waking process in the cold room of the animal A. The fine lines connecting the rings in I c, III b and III c are graphs of animals waking relatively undisturbed (thermocouple gently placed in the food pouch and the animal replaced rolled up in the nest). In the other graphs the animals were disturbed by being straightened out and by taking of heart beat in addition to temperature.

abrupt rise in the temperature curves at 5 to 10 minutes in the graphs. There is the same rate of increase in heart beat at about 25 or 30 minutes in the warmest room that was observed in the medium warm room ten minutes later. Heart beat may be more rapid at this time than when the from about 7° to about 27°, or 20° in 35 minutes, or 0.57°C. a minute. In the undisturbed awakening of two animals (Fig. 2, fine lines connecting the rings in IIIc) the rate of rise of temperature was about 19° or 20°C. in 40 minutes, about 0.5°C. a minute, after the rise was well begun.

Dubois (1896) gives some graphs of respiratory movements showing a rising rate as waking progresses. Other graphs of the waking dormouse showing pauses followed by a series of inhalations (Biot's type) and pauses followed by increasing depth of inspirations then decreasing again to another pause (Cheyne-Stokes respiration) were shown by Pembrey and Pitts (1899).

Several references to rate of temperature rise in waking were found in the literature. From these records the average rise has been calculated and is substituted here. For a portion of its waking period the bat may warm up about 1.1°–1.6°C. a minute (Pembrey and White, 1896; Pembrey, 1898). Ground squirrels (ziesels) may warm up 0.26° and 0.38°C. (Horvath, 1872a), 0.40°–0.45°C. (Horvath, 1878), or 0.30°C. (Mares, 1892) a minute. Dormice may warm up 0.37° (Pembrey, 1898) or 0.95°C. (Pembrey and White, 1896) a minute. Hedgehogs, which are larger, warm more slowly, 0.17° a minute (Pembrey, 1903), while the still larger marmots require three or four hours to warm from about 5° to 30°C., a rate of about 0.10° to 0.14°C. a minute. Most of these records were based on rectal temperatures and it has been shown that this lags far behind the esophageal, mouth or pouch temperatures (Quincke, 1881; Dubois, 1896; Mares, 1892; Shaw, 1925c; Johnson, 1929b; and others) and apparently catches up with the esophageal and pouch temperatures late in the waking process (Dubois, 1896; Johnson, 1929a, p. 179) especially in the cold room. This late rapid rise in rectal temperature appears to be produced largely by a sudden increase of circulation to that region after the anterior region has gradually warmed up from the beginning of waking, for Mares (1892) showed that jugular injection of indigo-carmine in a torpid ziesel quickly produced intense blue staining in the skin and mucous membrane anteriorly but not posteriorly. For the reasons given rectal temperatures are not reliable indicators of the rate of rise of metabolism but have been included here because they have some value in comparison between species.

The time required for waking from complete torpor depends somewhat on the size of the species. The following observations of waking time have been reported: (1) for the bat, 14 or more minutes (Pembrey and White, 1896; Pembrey, 1898), "a few minutes" (Adler, 1926), a half to one hour on the snow (Mangili, 1807), and three or four hours (Saissy, 1815; Quincke, 1881); (2) for the hedgehog, five to six hours (Saissy, 1815; Quincke, 1881); (3) for the marmot, three to four hours (Dubois, 1896), five to six hours (Quincke, 1881), and eight to nine hours (Saissy, 1815). These rates would probably be less variable if the observations had always begun at a certain body temperature and ended with the return of voluntary activity, and also if esophageal or food pouch temperatures had been taken.

The energy consumed in a unit time in waking ziesels has been stated to be 70 per cent greater than in the normal state (Mares, 1892). Mares found that during waking 5.9 gm. of oxygen per kilogram per hour were absorbed as opposed to 3.8 gm. in the normal state, and 6.0 gm. carbon dioxide are exhaled in waking compared to 3.9 gm. in the normal state. Pembrey and White (1896) noted the sudden increase in temperature just at the point of waking in bats, and this was observed to be accompanied by a much greater rate of heart beat and respiration at about the time of opening the eyes in ground squirrels (Johnson, 1929b) than was found after the animal was fully awake but not excited. The contraction of the heart, the movement of the thoracic muscles and the trembling, which may be present, appeared to account for the rapid rise in temperature in the latter part of waking. Mares (1892) considered that burning of fat produced this, but Dubois (1896) considered that glycogen in the liver was converted into sugar and this was burned. Further evidence of a great increase of sugar in the blood early in awakening has been submitted by Dworkin and Finney (1927). In waking there appears to be a vicious cycle. As the heart beat increases because of stimulation it is accompanied by more rapid respiration, both processes producing heat. Increased heat and greater muscle contraction both demand more oxygen. The excessive increase in metabolism in waking suggests to the author that the heat regulating mechanism is rather sharply brought into play after waking has progressed somewhat, for once the waking process is well started, placing the animal back in the cold and leaving it undisturbed almost never prevent complete awakening.

GOING INTO HIBERNATION

While the literature contains references to going into hibernation no exact data have been presented as to the physiological changes that occur, probably because study at this time almost invariably awakens the partly torpid animals. Dubois (1896) states that a marmot may wake in 3–4 hours, but requires 4–5 times as long to go into hibernation. Hatt (1927) states that a *Callospermophilus* might go into hibernation in 6 hours. Hibernation is always entered from a condition of normal sleep. The author took a great many food pouch temperatures of *C. t. pallidus* ground squirrels at intervals of one or two to several hours after the animals were placed in a refrigerator. The gentle picking up of the animal and careful insertion of the thermocouple in some cases did not prevent the

entrance into hibernation and the pouch temperature dropped from 1° to 3° an hour (Johnson, 1929c). Further work showed that it might drop 5°C. or even more an hour.

By taking temperatures thermo-electrically (illustrated in Johnson, 1929a) without disturbing the animal at all at the time the record was taken, drops of 6° to 7°C. an hour were observed for short periods in partly torpid animals in a rapidly falling room temperature, but the pouch temperature remained 1° to 2° C. above that of the room (Johnson, 1929c) even remaining 1°C. or more above when the room temperature stopped falling. From these data it was concluded that a fall in animal temperatures of 4°C. or more an hour was not uncommon.

The drop of 1° to 5°C. an hour in the early part of becoming torpid and up to 6° or 7°C in short periods in the later stages is very much slower than the rise of 20° in 35 minutes in rapid awakening in a very warm room.

CONDITIONS IN HUMANS RESEMBLING HIBERNATION

A considerable lowering of temperature in a hysterical person sleeping after being hypnotized was reported by Mares (1892). Fakirs in India have been often reported to be revived after months of burial underground (Busk, 1885; Mills, 1893, and others), but, while attested to by English officials, the possibility of deception by the fakirs has been raised (Hulk, 1885, and others). According to Claparède (1905), Cleghorn (1910) and other writers, in times of famine in some parts of Russia the peasants may conserve food by voluntarily sleeping for four or five months, doing only the necessary things and eating very sparingly. While metabolism is probably lowered in this way, it seems doubtful if there is much lowering of body temperature. Cushing and Goetsch (1915) have described symptoms of slightly lowered temperature and excessive adiposity in humans with deficient pituitaries and have considered this state related to hibernation. Mills (1892) also reported cases of excessive sleeping in two feeble minded men and in a woman who was tuberculous and had many adhesions of organs. Lowered temperature and drowsiness might, it would seem, be the effects of the illness rather than a condition resembling hibernation. Cases of lowered temperature in dying pocket gophers could easily be mistaken for real hibernation.

A CONSIDERATION OF THE POSSIBLE CAUSES OF HIBERNATION

There are certain outstanding facts regarding causes of hibernation. One is the existence of a large number of theories, summarized by Rasmussen (1916a). Another is the tendency of some writers to go to extremes in denying the causative influence of some possible factors. Thus cold has been declared not to be a cause of hibernation (Merzbacher, 1904, and others). A fact which must be kept in mind is that a poorly developed heat regulating mechanism is a prerequisite to the ability of a mammal to hibernate, and since this is essentially a pre-mammalian characteristic, we may consider hibernation as something retained rather than acquired by hibernating mammals.

Many authors have sought for a single cause for hibernation, but many conditions, both internal and external, may influence entrance into it. The possible external factors in hibernation will be considered first, and then the internal conditions which may influence it.

Temperature

Among the external conditions a low temperature has been considered a cause by many (Brown, 1847; Quincke, 1881; Adler, 1916), but many others have pointed out that only moderate cold is favorable for hibernation and animals may die below freezing temperatures (Mangili, 1807; Adler, 1916); or they may be awakened at first at about the freezing point of water (Dubois, 1896; Mangili, 1807; Pflüger, according to Merzbacher, 1904), or hibernation may even be prevented sometimes (Valentin, 1857). Sudden severe cold may irritate and finally kill the animal (Dubois, 1896; Johnson, unpublished). Others have shown that animals in captivity may fail to hibernate in winter, even if in a cold place (Mangili, 1807) but may hibernate in the summer or early fall in cool but not cold surroundings (Horvath, 1881; Wade, 1930; and others). Some dormice kept over winter by Forel (1887) failed to hibernate until May, but as they did not become fat until that time their failure to hibernate earlier may have been caused by a poor physical condition. Simpson (1911–12) considered that woodchucks wake in the spring without a higher surrounding temperature.

Perhaps no investigator who has had a large number of animals under observation at one time would deny that animals hibernate more in a room of about 5°–10°C. than in one of 20°–25°C., or even of 15°–20°C.

This has been the experience of the author, who recognizes, however, that cold is not the only cause, and that internal causes may aid hibernation in ground squirrels in cool weather (20°–22°C.) in the late summer, or hinder hibernation in cold weather (0°–10°C.) almost any time of year but especially in the spring. In outdoor pens in Chicago ground squirrels kept their burrows open until periods of cold weather and snow in December, 1915. Hahn (1914) observed this in nature.

The idea that heat may be a cause of hibernation (Brown, 1847; Merzbacher, 1904, quoting Cuvier and Buffon as authorities) in mammals appears to the author to be erroneous. It has previously been mentioned that no cases of hibernation have been seen in surrounding temperatures much above 20°—22°C., which must be considered low in comparison with the usual body temperature. The tenrec (*Centetes ecaudatus*) of Madagascar has often been cited as an animal that hibernates in the warm season but Milne-Edwards (1857–1863) cites evidences that it actually hibernates during the colder season.

Precooling

Koelsch (1925) and others have stated that animals cannot be made to hibernate in the summer by artificial cold and therefore the phenomenon is produced by internal factors only. While the work in this laboratory has shown conclusively that hibernation can be produced any time of the year, it must be admitted that there is less tendency to hibernate and greater mortality in the spring and early summer than in late summer (August), fall and winter. This is doubtless caused in part by internal factors but some evidence has been seen that it may be partly attributed to the previous season of hibernation, the poor conditions and greater excitability of new animals caught just before spring or summer study. It was also found that precooling ground squirrels nightly, as usually happens in the fall in animal quarters before the heat is turned on, caused them to go into hibernation significantly sooner when taken to a cold room than those which had not been precooled (Johnson, 1927, 1930). While precooling probably has facilitated the production of hibernation in the fall by various workers, it should not perhaps be considered a necessary cause in nature. However, intermittent or gradual cooling of the ground in the fall doubtless aids somewhat in preparing the animal for hibernation.

Food

Several authors consider starvation a cause of hibernation (e.g., Mangili, 1807; Hall, 1832; Forel, 1887; Simpson, 1912; Mann, 1916; Shaw, 1925c), but most of these men and others (e.g. Valentin, 1857) state that little food is eaten before hibernation even if it is present. The latter has not been borne out in ground squirrels in this laboratory. While the presence of food has often not prevented hibernation (Saissy, 1815; Mills, 1892; Wade, 1930) starvation has been found to make ground squirrels hibernate sooner than feeding (Johnson, 1925, 1930). Nineteen experiments in each of which six were fed and six starved and kept in the cold room from 7 to 23 days showed 13 per cent hibernation in the fed groups and 42.4 per cent in the starved groups. The fed groups showed an average of 78.5 per cent days before hibernation while the starved group went into hibernation after an average of only 42 per cent of their days in the refrigerator.

Dry Food

In order to test the theory advanced by Shaw (1925b) and Kashkarov and Lein (1927) that desiccation of vegetation produces aestivation 44 dry feed experiments were run by Kalaboukhov (1929) on 28 *Citellus pygmaeus* Pall. and 2 *Citellus fulvus* Licht. In these experiments there were 11 cases of hibernation in animals given dry feed but none in those given the same food soaked in water. Room temperatures during these experiments were from 12° to 22°C. No torpor occurred at temperatures above 22°C. Kalaboukhov remarks that the lethargy was identical to hibernation, which has also been the author's observation in numerous cases of torpor in the summer. Since no difference was noted no particular mention has been made of summer hibernation in the papers from this laboratory. Returning to Kalaboukhov's statement that no hibernation took place in the animals that had soaked food, it may be remarked that the author has had numerous cases of hibernation in July and August in a room of about 10°C. (a little colder than Kalaboukhov's temperature) among animals given green alfalfa or grass in addition to dry feed. For incidental evidences of this see Johnson (1930, Table I) and Johnson and Hanawalt (1930, Table II). The author has had numerous cases of partial hibernation following drops in room temperature for a night or for a few days in September. These animals hibernated in spite of water kept before them. A *C. t. tridecemlineatus* with a temperature of 31.0°C. in a room of 28.0°C. was only slightly torpid and could walk. Two *C. t. pallidus* at 28.0° and 20.2°C. in a room of 22.0° and 19.0°C. respectively could hardly move when taken up.

Wade (1930) performed some experiments on four *C. t. tridecemlineatus* outdoors and three indoors from July to October in which the animals had access only

to dry feed. His results would not support the conclusions of Kalaboukhov, for Wade's animals did not hibernate, although they lost much in weight. Since Wade's animals were doubtless at a higher temperature and mine were usually at a lower temperature than Kalaboukhov's, his results at temperatures of 12° to 22°C. are not contradicted by Wade's and mine. Furthermore, in a single experiment at 10°–15°C. nine *C. t. pallidus* ground squirrels fed only dry oats went into hibernation in an average of 3.8 days whereas ten fed soaked oats went in at 8.3 days.

Present data would seem to warrant a conclusion that dry food, as compared with moist, may serve as a weak cause of torpor. There is no question, of course, that dry hot weather followed by a drying up of the vegetation tends to drive the ground squirrels (Shaw, 1925b) and prairie dogs (Kashkarov and Lein, 1927) into their burrows, but once there it would seem that the quietness and coolness must aid in the production of torpor, if torpor is common in these animals in the summer.

Light

While many investigators have placed their animals in the dark to hibernate (Mann, 1916), light has not prevented hibernation (Wade, 1930, and others), and no influence on hibernation was found in 19 controlled experiments involving 12 animals each (Johnson, 1925, 1930b). It should be noted that the rolled up position of the animal in sleep and hibernation tends to shut out the light from the eyes even if it is present.

Confined Air

There appears to be no agreement as to the rôle of confined air in the production of hibernation. Mangili (1807) declared that it has no effect, but Bert (1868, 1870) produced a fall in temperature to 12°C. in dormice confined in a bell jar in the cold and Claparède (1905) considered that confined air would lower metabolism, aiding the change from sleep to torpidity. Brown (1847), Wade (1930) and others have mentioned hibernation in open air, but the former considers the lack of oxygen as a cause of hibernation.

In experiments involving 108 animals each in a half gallon can closed tight except for four nail holes about 3.0 mm. in diameter in the lid, the ground squirrels went into hibernation on the average after 19 per cent of their total days in the refrigerator had elapsed, whereas a similar number of controls in open cages hibernated only after 49 per cent of their stay in the refrigerator (Johnson, 1930). That this earlier entrance into hibernation was not produced by the more limited space of the half-gallon cans was shown by the fact that other controls in similar cans but with the tops highly perforated hibernated practically at the time and to the extent of those in the open cages.

In this connection we may consider Dubois' (1895, 1896) autonarcosis theory, which involves both external and internal conditions. He maintained that an excess of carbon dioxide in the blood is a cause of torpor. Torpid marmots to which he supplied a mixture of 12 per cent oxygen, 43 per cent air and 45 per cent carbon dioxide continued torpid until pure carbon dioxide was added at the beginning of the fifth hour, which caused the respiration rate of 3–5 a minute to double in ten minutes (1895). He concluded that a certain proportion of carbon dioxide would cause torpidity but that a greater proportion of it was responsible for waking. He also found that he could anaesthetize a dog in a mixture of air containing 17.3 per cent carbon dioxide (1901b). Rasmussen (1915, 1916b) found that the carbon dioxide content in the blood of the woodchuck was increased in hibernation, especially in the latter part of this state, but decreased again in waking. He also found that the difference in amounts of gases in the venous and in the arterial blood is greater in the torpid than in the normal animal. In two torpid woodchucks he found no increase in amount of carbon dioxide in the blood, indicating that Dubois' "autonarcosis" theory would not account for all cases of hibernation.

Obesity

Of the internal conditions, fatness has been agreed upon as a cause by practically all who have studied it as a possible factor (e.g., Horvath, 1881; Brown, 1847; Claparède, 1905; Mangili, 1807; Mills, 1892, 1893; Mann, 1916; Johnson, 1930; Wade, 1930). Lack of fatness has probably kept captive animals awake in the winter in some cases. Forel's (1887) dormice, for instance, did not hibernate until they became very fat in May, but from then until August they hibernated at a body temperature of 20°–22°C. A significantly greater amount of hibernation was found by the author in 38 heavy ground squirrels than in 118 light animals (Johnson, 1930) and the greater tendency of fat animals to hibernate has been observed in many animals in other experiments. Sometimes it would appear that very thin animals went into hibernation sooner than those of medium weight but closer study revealed the fact that such animals very frequently died after two or three days in torpor, so that their hibernation is not normal. Probably deaths reported by others as occurring when animals have been cooled in the summer have been due to thinness of the animals, and possibly also to the sudden transfer from hot to cold atmospheres.

Loss of Body Moisture

Loss of body water may be considered a possible internal cause, although it may be caused in turn by a dry food diet, which has already been found slightly conducive to hibernation. Since desiccation has been found to favor hibernation in the potato beetle (Tower, 1906; Breitenbecher, 1918; Fink, 1925) and also to produce cold hardiness in insects (Bodine, 1923; Payne, 1927) it is interesting to note that Dubois (1895, 1909) found that the blood of torpid marmots was somewhat desiccated. Rasmussen (1915, 1916c) found an increase of 5 per cent in erythrocytes in hibernation and a 20 per cent decrease after the woodchucks had eaten and drunk, indicating a tendency to desiccation in hibernation. It is concluded by Gorer (1930), however, that the water balance is not uniform in hibernating mammals.

Hypofunction of the Thyroid Gland

Histological work on the thyroid of ground squirrels, *C. t. tridecemlineatus*, (Mann, 1916; and Peiser, 1906, according to Gorer, 1930) led to no evidence of a relationship to hibernation, but did show a flattening of the cells and a great diminishing of colloid in the fall. Adler (1910a) found histological changes in thyroids of bats and hedgehogs that indicated excessive secretion of colloid just after waking in the spring and this was later confirmed by Coninx-Girardet (1927). Subcutaneous injections of extracts of thyroid and also of thymus and suprarenals were found usually to produce waking in the hedgehog by Adler (1910a, 1916). From other experiments in which the heat regulating center had been removed and the sympathetic nervous system deadened with ergotoxin he concluded that these substances produced waking by increasing oxidative processes at the periphery and not wholly by action on the heat regulating center or on the sympathetic nervous system (Adler, 1910b, 1916). Schenk (1912) also found the same extracts produced a rise in metabolism and sometimes a waking in torpid hedgehogs. Zondek (1924), however, produced waking not only with Adler's extracts but also with others including physiological salt solution of a temperature of 8°C. or more above the rectal temperature of the animal and concluded that the warmth and not the specific nature of Adler's extracts produced waking.

Intra-peritoneal injections of very large doses of thyroxin (31 to 52 times the human dose considering comparative body weights) in 66 *C. t. pallidus* and feeding of thyroid substances to 23 produced no inhibition of hibernation over that of the controls (Johnson and Hanawalt, 1926, 1930). From these experiments it appears that the thyroid does not prevent hibernation and that the increased activity of the gland in the spring, shown by Adler (1910a) and Coninx-Girardet (1927) is not the cause of waking but accompanies it, possibly as a result.

Adrenal Glands

Adler's (1910a) work indicating an inhibitory effect of an adrenal extract as well as thyroid and thymus extracts and Zondek's (1924) refutation of it have already been mentioned. Enlargement of the adrenals of *C. t. tridecemlineatus* in the spring was reported by Mann (1916), but little change except an enlargement of the blood vessels was found in these glands in the winter (Coninx-Girardet, 1927). Britton (1928) has shown that in artificially cooled cats the presence of the adrenals is necessary for spontaneous awakening from this condition of torpor and suggests that waking from hibernation is produced by increased "sympatico-adrenal" activities, whereas entrance into hibernation is caused by decreased activity.

The Pituitary Gland

Gemelli (1906) observed no change in the posterior lobe but in the anterior he found a great decrease in number of "*cianofile*" cells in hibernation in the marmot. Cushing and Goetsch (1915) observed drowsiness and a lowering of temperature, respiration and heart beat in humans with diseased pituitaries. They also found reduction in size of the ductless glands, especially of the anterior pituitary, in hibernating marmots and a production of fatness and drowsiness in a young hypophysectomized dog. Mann (1916) found no constant change in the pituitary associated with seasons in the ground squirrel. Rasmussen (1921) found no changes from fall to winter in woodchucks but found indications of increased activity in the spring. Coninx-Girardet (1927) found an increase in number of basophile cells in the woodchucks in the spring including the breeding season, which also indicated increased activity of the pituitary at that time. In the winter decreased activity was indicated by a reduction in number of basophile cells and by a more open grouping of the cells of the pituitary.

While the histological appearance of the anterior pituitary indicates renewed activity in the spring it should be noted that this might be a result and not a cause of waking and only physiological experiments can give conclusive evidence. Experiments in this laboratory with a weak extract by B. R. Coonfield and the author showed no effect on hibernation. More recently a stronger alkaline extract has shown some inhibitory action and subcutaneous injection of cut

pieces of the pituitary into 20 ground squirrels has shown marked inhibitory effects on entrance into hibernation.

No evidence has been produced which indicates that the posterior pituitary has any influence on hibernation; on the contrary, the injection of pituitrin by Johnson and Hanawalt (1926, 1930) gives definite evidence that it has neither an inhibitory nor a causative action on hibernation.

Gonads

Gonadal enlargement in hibernating forms in the spring has been found by Mann (1916), Drips (1919), Rasmussen (1917, 1918), Shaw (1926) and Johnson (1930). Mann showed that castration did not prevent hibernation in *C. t. tridecemlineatus*. That gonadal activity tends to prevent hibernation in the spring but not at other times of the year has been shown by Johnson (1927, 1930) in *C. t. pallidus*, for castrated animals hibernated to a significantly greater extent than did normal animals during the breeding season. It was also recognized that this activity is probably caused by increased secretion of the anterior pituitary.

Other Possible Causes Investigated

Removal of the spleen was found to show no effect on hibernation by Mann and Drips (1917), although they found the vessels much congested. Extracts of the thymus used by Adler (1910a) produced waking from hibernation, but this work was questioned by Zondek (1924), and other work seems to raise the question whether this structure is an endocrine organ. Structural differences between hibernators and other animals were sought by Mangili (1807), who considered that the arterial blood supply to the brain was small in hibernating forms, and by Saissy (1815), who stressed the large blood vessels of the thorax and abdomen, small peripheral vessels, large nerves to the head, and limited blood supply to the brain as characteristic features in hibernating forms. While many authors have noted the lack of peripheral bleeding when a hibernating animal is cut and have seen the congestion in the chief blood vessels, it would not seem that these can have a causative relation to hibernation.

Injection of insulin sufficient to produce hypoglycemia caused woodchucks, dogs and cats to pass temporarily into a state of torpor (Cassidy, Dworkin and Finney, 1925a, b; Dworkin and Finney, 1927), in which the respiratory quotient fell in the dogs as if they were in true hibernation (Finney, Dworkin and Cassidy, 1927). Injection of adrenalin and pituitrin brought back the shivering reflexes in partly torpid animals that had ceased to shiver (Cassidy, Dworkin and Finney, 1926). Whether these observations reveal any internal causes of hibernation it is difficult to say. It would be interesting to know whether the blood sugar level of an animal that falls into hibernation very readily is different from that of one that shows great resistance to hibernation in a cold room.

The inhibiting effect on hibernation of external stimuli has long been recognized. Thus Dubois (1896) found that the taking of temperatures of the marmot tended to shorten its hibernating period and Brown (1847) found that excitability kept animals awake.

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THE THREE TYPES OF MORTALITY CURVE

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THE death-rates of different organisms are compared by Pearl (1) by plotting the number of survivors on arithlog paper. In this, as our figure shows (Fig. 1), the abscissal scale is divided arithmetically, and the scale of ordinates geometrically. The abscissa indicates age, but Pearl subdivides the life span of each organism into centiles, and thus he compares the different life spans of different organisms on a single graph. The ordinate signifies the number of survivors. It shows, therefore, how many individuals out of 1,000 living at age 0 are alive at successive ages, expressed as centiles of the life span. On reaching the one-hundredth centile, the last individual dies and the curve touches the abscissal axis. Now Pearl states that, theoretically, three types of the curve can be imagined. The first is the rectangular type, referring to individuals who live for about the same period and die at the same age. This type is approximated by the life curve of *Proales decipiens*, of present-day man, and of wild Drosophila.

The second type is the diagonal, which is represented on arithlog paper by a straight line; the death-rate is constant from the beginning of life to its end. This type is approximated by the life curve of vestigial Drosophila.

In the third type there is a large initial death-rate; the curve declines sharply at the beginning of life, and then runs almost horizontally until the end of the life span. Pearl reports in his work of 1928 that he has never actually happened to observe this type of life curve, which may be imagined theoretically.

In this short paper I take the liberty of pointing out that the mortality curve of forest trees is an example of this third type, which I should like to name the hyperbolic type, as it is hyperbola-shaped.

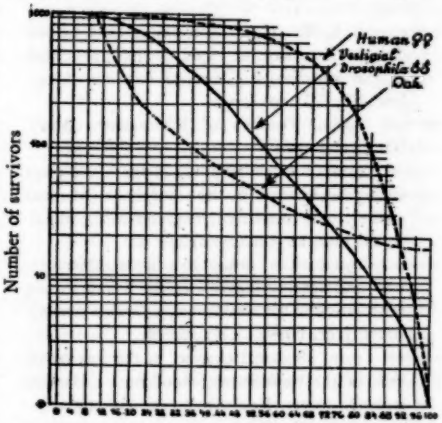

FIG. 1. SURVIVORSHIP CURVES OF MAN, OF VESTIGIAL DROSOPHILA, AND OF THE OAK

The first two are after Pearl, *The Rate of Living*, A. A. Knopf, N. Y., p. 43; the third is based on Fekete's data.

In Figure 1 are shown the life curves of man and vestigial Drosophila (from Pearl, p. 38), together with that of the oak, based on the data of Fekete. There are no data for the latter under twenty years or above 200 years. However, the observed part of the curve has a form corresponding to Pearl's theoretical third type of life curve.

According to Pearl, the curves should

start at biologically equivalent ages. He therefore begins the Drosophila curve at the first day of imaginal life and the human curve at the twelfth year of life, as the death-rate is then a minimum. In the hyperbolic type this condition can not be fulfilled, since the death-rate shows no minimum near the beginning of life.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

COPE: MASTER NATURALIST. *The Life and Letters of Edward Drinker Cope with a Bibliography of His Writings Classified by Subject. A Study of the Pioneer and Foundation Periods of Vertebrate Palaeontology in America.*

By Henry Fairfield Osborn with the Co-operation of Helen A. Warren, and Citations from the Writings of George Brown Goode, Theodore Gill, Persifor Frazer, Henry Fairfield Osborn, William Berryman Scott, William King Gregory, William Diller Matthew.

Princeton University Press

$5.00 6 x 9¼; xvi + 740 *Princeton*

In this book Professor Osborn has made an outstanding addition to his already long and noteworthy list of biographical writings. Edward Drinker Cope was in some ways the most romantic figure in the history of American science. Undoubtedly a genius, he had a colossal capacity for work coupled with great intellectual brilliancy and originality. These qualities in themselves were enough to cause a plenitude of difficulties in an American academic career. But over and beyond the troubles which were caused by these elements in his own make-up Cope suffered the misfortune of arousing first the jealousy and then the bitter enmity of a rich and academically powerful paleontologist, whose complex character cannot be accurately or adequately described in a farm and garden magazine such as this, even though the National Academy of Sciences did see fit to make him its president. It must suffice to say that the later part of Cope's life was full of troubles and difficulties. This is, of course, a familiar and ever-recurring story in the history of science, and, indeed, in the history of mankind generally. Like many geniuses, and not a few other folk, Cope was in some respects a foolish fellow. This helped to his undoing. But happily time has already given him a fairer and sweeter fame than lingers about the memory of some of those who opposed him and who got most of the breaks during life.

The great value of this book primarily arises from the fact that Cope's daughter made available to Professor Osborn all of her father's letters and papers. With masterly skill these have been put in order, edited, and amplified so to tell effectively, clearly, and honestly the story of a great life. This volume, coupled with the

National Academy biographical memoir on Cope by the same author, together make a fitting and adequate record. Biologists will always be grateful to Professor Osborn for this splendid piece of work.

LECTURES ON DARWINISM

By Arthur Willey *Richard G. Badger*
$2.00 5¼ x 7¾; 198 *Boston*

The title of this book is a trifle misleading, in that relatively little space is actually devoted to Darwinism, in the sense of natural selection. The book, however, is reminiscent of the Darwinian style in its constant preoccupation with illustrations from concrete biological observations. The author's concluding paragraph runs:

> If we can see no particular future advances in store for natural selection it is because one cannot help feeling that its work is mainly accomplished, both as a factor and as a theory. It cannot contribute any more than it has done already to solve the riddle of human life nor to improve the status of wild life. As a doctrine it is an achievement of the nineteenth century, as an aid to evolution it is a monument of the past and has hardly more direct bearing upon twentieth century life than has Cleopatra's Needle. It explains the origin of species up to a certain point but accounts in still larger measure for the relative constancy of established species. The apparent fixity of species could easily be mistaken for absolute fixity and this erroneous idea persisted up to the period which witnessed the simultaneous publication of the independent works of C. Darwin and A. R. Wallace. Its worst fault is that it cannot be verified experimentally, while there are many other biological problems which are amenable to experimentation. From being a hotly contested issue it has become a hollow truth, like the bowl of the Eastern Sage, chiefly valuable because of its emptiness.

THE PROBLEMS OF EVOLUTION

By Arthur W. Lindsey *The Macmillan Co.*
$2.00 5 x 7¼; xiii + 236 *New York*

An attempt at a restatement of the problem, more particularly with reference to the old question of heredity and environment. The author emphasizes the position (which seems almost self-evident to us) that the actual characters of an organism are necessarily the result of the interaction of both factors. He believes that there is still room for experimental attempts to show that evolutionary changes can be produced under the stimulus of changed environment.

GENETICS

SELBSTSTERILITÄT UND KREUZUNGSSTERILITÄT IM PFLANZENREICH UND TIERREICH

By Friedrich Brieger *Julius Springer*
33.80 marks (bound) *Berlin*
32 marks (paper) 5⅝ x 8½; xi + 395

Besides the cases of true sterility, in which no functional gametes are developed, there are numerous cases, especially in plants, when gametes which are fertile in certain combinations fail in others to combine into a zygote. To this phenomenon, which may prevent on the one hand self-fertilization or on the other hand crossing, Dr. Brieger gives the name parasterility. There are various ways in which this may happen. In plants the pollen may be prevented from reaching the stigma, or having reached it, may not sprout normally; the pollen tubes may be retarded in their growth through the tissues of the style, or having reached the ovary, may not be attracted to the ovules; or finally, the pollen nucleus may not unite with the egg nucleus. In all cases there is a disturbance of the normal relations between the male and female elements. There is no relation between the systematic position of a species and the sterility phenomena which it displays.

Dr. Brieger is sceptical of the teleologi-

cal character of self-parasterility, since it shields unfavorable recessive characters from the action of natural selection.

RACIAL INVESTIGATIONS. X. *The Atlantic Cod (Gadus callarias* L.*) and Local Races of the Same. Comptes Rendus des Travaux du Laboratoire Carlsberg. 18me Volume No. 6*

By Johs. Schmidt *Laboratoire Carlsberg*
5 Kr. *Copenhagen*
6 x 9½; 72 + 10 plates (paper)

An investigation of variation in the cod, based on about 20,000 specimens from 114 stations, covering the greater part of the region of occurrence of the species in the Atlantic. The characters studied were the number of vertebrae and the number of rays in the second dorsal fin. It is found that there are considerable local variations in both characters. There is a distinct correlation between temperature and the variables studied in the open sea stations, a lower temperature being associated with increases in number of vertebrae and dorsal fin rays. There is no direct evidence as to the mechanism of the association.

DIE SEXUELLEN ZWISCHENSTUFEN

By Richard Goldschmidt *Julius Springer*
45 marks (paper) *Berlin*
46.40 marks (bound)
5½ x 8¼; x + 528

This exhaustive study of intersexuality and gynandromorphism will be of great interest and importance to workers in genetics. The author presents his own work with *Lymantria* in detail, as being the most completely understood case; and then summarizes the results obtained with other forms, and attempts to bring them in line with his theory of the physiological action of the genes.

THE PRACTICAL DOG BOOK. *With Chapters on the Authentic History of All Varieties Hitherto Unpublished, and a Veterinary Guide and Dosage Section, and Information on Advertising and on Exporting to All Parts of the World. A Comprehensive Work Dealing with the Buying, Selling, Breeding, Showing, Care, and Feeding of the Dog.*

By Edward C. Ash *The Derrydale Press*
$7.50 6⅛ x 9⅜; xxxii + 343 *New York*

This book contains histories of all breeds, a complete guide on feeding, breeding, and showing, and other information. To dog lovers of an antiquarian turn of mind the many illustrations from early books will be of interest. A useful reference work for the genetics library.

GENERAL BIOLOGY

A BIOLOGICAL STUDY OF THE OFF-SHORE WATERS OF CHESAPEAKE BAY. *U. S. Department of Commerce, Bureau of Fisheries Document No. 1091.*

By R. P. Cowles
U. S. Government Printing Office
30 cents 7½ x 11; 104 (paper) *Washington*

Chesapeake presents many interesting biological problems. In shape it is a long, narrow body of water (160 nautical miles in length, 5 to 20 in width) extending almost directly north and south in the states of Maryland and Virginia. A fairly narrow opening (10 miles in width) at its southern end gives outlet to the Atlantic Ocean. Two large rivers, the Susquehanna and the Potomac, and numerous smaller rivers, empty their waters into the bay. In addition there are numerous bays, sounds, and small inlets. Although in general the bay is rather shallow, 30 or 40 feet being about the average for deep water, there are far deeper areas along the eastern shore. While there are no very strong currents in the water yet there is an

ever changing condition due to the inflow of many rivers, the ebb and flow of the tide, eddies, and currents of water moving in more or less opposite directions at the surface and bottom in the same locality. In addition there are the seasonal changes in temperature, rainfall, and strong winds.

The survey, which covers a period of several years, has already yielded much of importance. Thirty widely distributed areas have been visited at intervals. Collection and identification of the plants and animals have been made to ascertain their distribution and abundance. Environmental conditions have been recorded. Studies in salinity, temperature and plankton content will, as the survey continues, yield much needed information on the laws which govern the migration of fishes and crabs in the bay. It is expected that knowledge of the normal conditions of the bay will be of great aid in ascertaining what unusual changes have occurred during those years when there has been a great mortality of fishes, oysters, crabs and clams, food products which are a great economic asset to the two states.

The paper includes charts exhibiting the changes of salinity and temperature in different areas and seasons, and a lengthy bibliography.

A YEAR ON THE GREAT BARRIER REEF. *The Story of Corals and of the Greatest of Their Creations.*
By C. M. Yonge *G. P. Putnam's Sons*
$6.00 *New York and London*
6¼ x 9⅜; xx + 246

This delightful book is a by-product of the Great Barrier Reef Expedition of 1928–29. The party under Dr. Yonge's direction had its headquarters at Low Isles, and was principally engaged on experimental researches on such matters as growth, respiration, and feeding of coral, etc. The technical results of these and other investigations of the Expedition will be published in a series of official reports. What the present book does is to give a superb popular account of the biology of corals; the formation of coral reefs; the extraordinary *congeries* of animals other than corals, and the plants, which together make up the biota of a coral reef; and finally the characteristics of the Great Barrier Reef, the longest in the world. The illustrations are numerous and extremely well done, particularly the halftone plates, which attest the photographic skill of Mrs. Yonge, the Medical Officer of the Expedition, evidently a most versatile person.

We commend the volume unreservedly. Every school and college library should have it.

GROSSE BIOLOGEN. *Eine Geschichte der Biologie und ihrer Erforscher.*
By Ernst Almquist. *J. F. Lehmanns Verlag*
6.50 marks (paper) *Munich*
8 marks (bound) 6 x 8⅛; 143

Professor Almquist writes on a different plan from that of many historians of science. His book is as much a critique as a presentation of the discoveries and theories of the great biologists. He feels that, under the influence of Darwinism and democracy, too little attention is paid to the constancy of species. Lamarckianism, the mutation theory, Darwinism, are all probably partial aspects of the truth.

In his account of Linné the author brings out the fact that, though in his *Fundamenta Botanica* Linné had assumed that species were originally created in their present forms, in later publications he suggested that new species might have arisen through crossing.

ANIMAL AGGREGATIONS. *A Study in General Sociology*
By W. C. Allee *University of Chicago Press*
$5.00 6 x 8¾; ix + 431 *Chicago*

The social insects have long been the subject of intensive study; but so far as we are aware no one has devoted a book to what one might call sub-social life. There have been many scattered observations on the physiological results of animal aggregations, and an increasing number of workers have devoted attention to one or another phase of the problem of the influence of animals in proximity upon each other. Doctor Allee has been one of the pioneers in the systematic study of the subject, and in the present volume he has assembled a variety of phenomena from the literature and from his own experience. He particularly emphasizes the fact that there may be beneficial as well as harmful effects of crowding—a point that escaped many of the earlier observers.

The book will be disappointing to those who like neat solutions to their problems. Most of the problems remain without solution, for the present at least. But for anyone in search of problems, the book will be a joy; any chapter will offer the young researcher problems to last his next ten years.

Our only serious quarrel with the book is that the author is not rough enough. Our own reading of some of the work in this field has left us very dubious as to its real soundness, and we feel that it would have been better to have pointed out more of its shortcomings than Doctor Allee has done.

A NATURALIST IN A UNIVERSITY MUSEUM
By Alexander G. Ruthven
Alumni Press, University of Michigan
$5.00 6½ x 8½; 143 *Ann Arbor*

A plea for the usefulness of museums in general, and university museums in particular, with statements of the policies best adapted to enable the museum to perform its functions most effectively. There are also some reflections on the kind of biology which should be taught in the secondary schools, and on the training of secondary school teachers, which seem to us sound and valuable.

GARDEN POOLS *Large and Small.*
By Leonidas W. Ramsay and Charles H. Lawrence *The Macmillan Co.*
$2.50 5½ x 8½; xiv + 108 *New York*

A useful guide for the amateur who builds his own pools. It contains all the necessary information concerning the building of garden pools, stocking them with plants and aquatic animals, care of water, mosquito control, etc. The author has made those sections dealing with types of plants to select for the pool, pool margins, and background and their cultural requirements especially helpful. The book is excellently illustrated with photographs and diagrams showing pool construction and what decorative effects to aim for. There is an index.

ESSENTIALS OF BIOLOGY
By W. H. D. Meier and Lois Meier
Ginn and Co.
$1.68 5 x 7½; vii + 529 *Boston*

This excellent text-book for schools emphasizes the interrelation of organisms with each other and with the physical world about them, the way in which each organism maintains its own life and the life of the species, the conservation of native plant and animal life, the development and improvement of living organisms, and their control for the health and well-being of man.

GRENZFRAGEN DES LEBENS. *Eine Umschau im Zwischengebiet der biologischen und anorganischen Naturwissenschaft*
By Friedrich Rinne *Quelle und Meyer*
9 marks (paper) *Leipzig*
10 marks (cloth)
$6\frac{3}{4}$ x $9\frac{3}{4}$; vii + 128

A survey of the relations between the organic and the inorganic. The author concludes that there is no sharp line of division between the two realms and that some day life may be produced in the laboratory.

HUMAN BIOLOGY

THE STONE AGE CULTURES OF KENYA COLONY
By L. S. B. Leakey, with Appendices by J. D. Solomon, C. E. P. Brooks, A. T. Hopwood, H. C. Beck, and M. Connolly
The Macmillan Co.
$9.00 $7\frac{3}{8}$ x $9\frac{3}{4}$; xiii + 288 *New York*

This beautifully produced book opens a new chapter in archeology. While the work which it records has only just fairly begun it already gives distinct promise of leading to the establishment of a definite correlation between European and African prehistory. The basis of such a correlation is the climatic changes in the Pleistocene era. Evidence is accumulating to indicate that the glacial and interglacial periods in Europe had as counterparts in Africa pluvial and interpluvial periods, that is wetter and dryer periods. These suggested correlations are tabulated (p. 232) as follows:

Nakuran wet phase	Wet period *circa* 850 B. C.
Dry period	Climatic optimum
Makalian wet phase	Bühl stadium, etc., to climatic optimum
Dry period	Achen retreat, etc.
Gamblian pluvial. The sub-divisions are Lower Gamblian and Upper Gamblian with a mid-Gamblian pause	Würm glacial Riss-Würm inter-glacial Riss glacial
Long break with periods of faulting and volcanic activity	Mindel-Riss inter-glacial
Kamasian pluvial. Sub-divisions unknown but may include Mr. Wayland's Kafuan and Sangoan	Mindel glacial Günz-Mindel interglacial Günz glacial

The present volume gives the general archeological results of the first two seasons' excavations of the East African Archeological Expedition under the author's direction. The skeletal remains found are being worked up under the guidance of Sir Arthur Keith, and will form the subject of a later volume.

The work so far done shows beyond any possibility of doubt that many of the stone cultures of Europe have also existed in Kenya. But whether they existed at the same times in Europe and Africa has not yet been definitely settled.

Extreme care and thoroughness, coupled with commendable caution in drawing conclusions, characterize the work. The work is extensively and beautifully illustrated, chiefly with photographs and drawings of the artefacts found. There are several appendices: one on the geology of the region studied, by J. D. Solomon; the second on climatic correlations, by C. E. P. Brooks; the third on fossil mammalia found; by A. Tindell Hopwood; the fourth on mollusks, by M. Connolly; and the fifth on prehistoric man in East Africa, by Prof. J. W. Gregory, who was the first European to find a stone age tool in Kenya.

Altogether this is a contribution of first class importance to human prehistory.

THE PHYSICAL BASIS OF PERSONALITY
By Charles R. Stockard
W. W. Norton and Co., Inc.
$3.50 5¾ x 8¼; 320 *New York*

In this book Professor Stockard deals, not only with the constitution of the adult, but with the hereditary and environmental factors which influence the complex process of embryonic development. The hereditary composition, which is unique for each individual, contains the potentialities of the personality, but in order to develop this personality a long series of interactions with the environment must take place.

There is no question here of the degree of importance between the genetic background and the developmental environment; neither is sufficient without the other. Without genetic basis there is no individual, and without a suitably arranged complexity of environment the complete genetic basis is unable to produce the normal individual. The interaction between the individual and the environment is continuous from the germinal beginning to the end of life, and it is mutual: each modifies and affects the other. The individual and the environment are not separate; they are parts of a larger arrangement.

In particular, changes in rate of development may have a profound influence on the finished product. If the embryonic development of an organism is retarded at a critical moment for a particular organ that organ may permanently lose its normal relation to others. Professor Stockard believes that these changes in rate of development are often caused by changes in the endocrine secretions. Thus the achondroplasic legs of dachshunds and basset hounds may be due to a hereditary disturbance of pituitary gland secretions acting only during a critical moment in the development of the embryonic limbs, while the achondroplasic skulls and vertebral columns of bull-dogs are due to a similar disturbance acting at another time. This may or may not be the secret of the matter. Endocrine changes in the embryo are easy to postulate but difficult to check.

As to mankind Professor Stockard classifies them in two main types, the linear or long-headed, and the lateral or wide-headed, and suggests that they depend on differences in thyroid activity.

POSTURE AND PHYSICAL FITNESS
United States Department of Labor, Children's Bureau Publication No. 205
By Armin Klein and Leah C. Thomas
U. S. Government Printing Office
10 cents *Washington*
5⅞ x 9⅛; v + 45 (paper)

Important and interesting results have been obtained in this investigation on the effect of good body mechanics on the health and efficiency of grammar-school children. The training was given in the Williams School at Chelsea, Mass. The posture training group included 961 children. A control group of 747 received only the regular gymnastic training. The two groups were similar at the first examination in respect of age, sex, nationality, and posture grade and various physical indices. The children were mainly from the Russian Jewish district. Unfortunately space only permits a few of the findings to be mentioned. Among these are:

"At least 80 per cent of the children in each age period had poor posture. The children of the broad type of body physique had the largest percentage of good posture, and those of the thin type had the largest percentage of poor posture.

"The prevalence of poor body mechanics was strikingly reduced by posture training. During the period of observation six children in the posture class improved in posture to every one of the control children who improved."

"Good posture once acquired was maintained, on the whole, over the 2-year period of observation by the children who received two years of posture training.

"Improvement in body mechanics was associated

with improvement in health and efficiency. More of the children who started with poor posture, when given training, improved their nutrition when they improved their posture than did those who did not improve their posture."

"Improvement in body mechanics was also associated with improvement in school work. The rate of absence due to personal illness decreased in children who received posture training until it was considerably lower than that of untrained children."

"Posture training and better posture brought an improved sense of muscle position and, therefore, improved ability to direct retraction of the lower abdomen. This ability is of value in that, with practice, the retraction of the lower abdominal wall becomes habitual and steady."

"About four-fifths of the children observed had pronated feet. This condition was most frequently associated with poor body mechanics. It was more frequent among children of the thin type and was less frequent among children with good nutrition."

The records of the data collected are exhibited in graphs and tables in the paper. In an appendix is given the physical examination schedule used in the study.

CHILDREN OF WORKING MOTHERS IN PHILADELPHIA. *Part 1. The Working Mothers. United States Department of Labor, Children's Bureau Publication No. 204*
By Clara M. Beyer
U. S. Government Printing Office
10 cents *Washington*
5¾ x 9; iv + 39 (paper)

The report of this survey is divided into two parts. The present bulletin dealing with "The mothers" will be followed later by one on "The findings about the children of these working mothers."

The study was undertaken mainly to ascertain the relationship between the employment of mothers and the welfare of their children, but much collateral information was gleaned concerning the increasing tendency of mothers to be employed outside the home. The field survey was made in eleven districts in different parts of Philadelphia in 1928, between the months of January and September. For purposes of comparison information concerning non-working mothers and their children living in the same districts was gathered. Not only were the mothers interviewed but social agency, court and school records were investigated. Among some of the conclusions which are reported in this publication are the following:

The employment of mothers is affected by various factors, among the most important of which are race, nativity, nationality, and age and number of children. Of the 6,070 mothers interviewed who had one or more children under 16 years of age and had worked after marriage, 4,486 (74 per cent) were white and 1,569 (26 per cent) were negro; 51 per cent of the white mothers were foreign born. Work was less frequent among the native-born white mothers than among the foreign born and negro. However, some of the foreign-born groups—notably the Irish, Italians, and Jews—showed a marked disposition for the mother to stay at home with her children. . . . . The proportion of mothers employed varied directly with the number of children and with the presence of children of preschool age.

The report includes fifteen tables listing the data gathered. In Appendix A is given a description of the different districts surveyed and a discussion of the employment of mothers in these districts. In Appendix B are tables showing the employment of the mothers in these districts.

DJUKA. *The Bush Negroes of Dutch Guiana*
By Morton C. Kahn *The Viking Press*
$3.50 5¾ x 8¼; xxiv + 233 *New York*

This unique group of negroes are descendants of slaves transplanted from West Africa to Guiana by the Dutch in the latter part of the seventeenth and the early part of the eighteenth centuries. The jungles of South America furnished a safe hiding place for those who managed to escape bondage. By the year 1749 so powerful had the group become that the Dutch

were obliged to make a treaty with them which gave them their independence and in addition an annual tribute. The negroes, being a proud and hardy race, have maintained their tribal government up to the present time and still receive from the Dutch officials the yearly sum of money.

The author of this book, a bacteriologist, first went to the South American tropics in 1922 to study public health measures as applied to tropical diseases. He has since made several trips for the purpose of studying the Djukas. He writes entertainingly of his experiences and observations. Anthropologists and ethnologists will find much interesting material in the book, especially in those chapters on the dance, marriage and the family, medicine and magic, Djuka talk, and West African survivals. The Djukas are very skilful in wood carving and among the many illustrations of the book are interesting examples of this art. The author includes a sketch-map, sections on phonograms and symbols, a bibliography and an index.

EDUCATION, CRIME, AND SOCIAL PROGRESS

By William C. Bagley *The Macmillan Co.*
$1.20 $4\frac{3}{4}$ x $7\frac{1}{4}$; xv + 150 *New York*

This notable book will deeply interest many parents and educators who have been distressed by the trend of education in the United States. Prof. Bagley says in his introduction:

> In sharp contrast to education in most of the civilized countries, an outstanding characteristic of education in the United States is its virtually complete rejection of the disciplinary ideal in the fields both of mind and of morals. As will be shown in the following pages, the rejection of mental discipline as an ideal was not entirely—nor even chiefly— due to the teachings of educational theory. Nor is the rejection of the disciplinary ideal in the field of morals to be charged entirely against the theorists. In both cases, and in a quite real sense, theory has served to rationalize and justify a certain—although a somewhat inarticulate—popular demand. This condition will make it difficult to correct what is, in the writer's judgment, by far the most serious weakness of American education and the weakness with which this book will be primarily concerned.

The book contains a collection of papers, a number of which have been given as addresses before educational meetings, etc. The headings of the chapters are as follows: Two outstanding problems of American education; Some handicaps of character education in the United States; Discipline and dogma; Shibboleths and slogans in educational reform; Playing at the work of education; Through discipline to freedom; Emergent idealism; Education for adaptability.

Professor Bagley does not discard as without value many of the innovations which have crept into modern educational methods. He finds much that can be of ultimate good provided the present tendency to follow "fashions with a maximum of zeal and a minimum of discrimination" can be avoided. If this book could be used as a text for study in parent-teacher organizations and mother's clubs, as well as in more advanced educational groups for a period of several years it would have profoundly useful effects. For it is a first-rate book, full of sound sense and ripe wisdom. We recommend it to all our readers.

BIOLOGY IN HUMAN AFFAIRS.

By Walter V. Bingham, Hugh S. Cumming, Edward M. East, Morris Fishbein, Frank H. Hankins, Joseph Jastrow, Donald F. Jones, E. Kennerly Marshall, Jr., Elmer V. McCollum, Howard M. Parshley, Arthur M. Stimson, Lewis M. Terman. Edited by Edward M. East.

Whittlesey House, McGraw-Hill Book Co., Inc.

$3.50 5⅜ x 8⅜; xxi + 399 *New York*

This book discusses what biology has to offer to man in his attempt to solve the problems which his mind and his body pose for him. The chapters deal with the following topics: Biology and human problems; the prospects of the social sciences; the renaissance of psychology; educational psychology; psychology in industry; heredity; the frontiers of medicine; the outlook of public health work; physiology of to-day; zoology and human welfare; efforts to increase the food resources; diet and nutrition. In the first essay Professor East pays his respects to those who have suggested that the scientific method may not be the only way of arriving at truth.

As to there being true scientists whose tenets include belief in the possibilities of attaining knowledge through some mysterious insight which differs from all ordinary percepts and their rational consideration, I simply deny the allegation. It is a mistake to assume that when Millikan, K. T. Compton, and Pupin issue preachments in terms of theology and metaphysics, they are speaking as scientists. They are merely demonstrating how difficult it is to divest one's mind completely of the whams and whimseys learned in early childhood. These men are competent physicists who have done admirable work in their own bailiwick by using the objective methods of science. This procedure has worked well in the solution of the problems in which they have been interested. Through it they have been successful. By its means they have attained fame. Do they give honor where honor is due? Oddly enough, they do not. In their leisure hours they endeavor to show that the perplexing questions which concern man most intimately—problems of emotion, of conduct, of thought—are unassailable by these time-tried methods. They speak vaguely of man's higher nature, something above the rational, which may attain to truth by mysterious inspiration. And they are speaking of man, you understand, of that animal of the family Hominidae, whose corporeal make-up is better known than that of any other organism; whose functional activities have been the subject of experimentation for a century and a half; whose hopes, whose desires, whose emotions, whose mental peculiarities are objective problems about which the psychologist knows almost as much as the physicist knows about the atom; and all through the application of scientific methodology. In other words, these men who have become distinguished by using scientific methods in a given field, turn to a department in which they have no accurate knowledge and maintain seriously that here the primitive folklore of the race, unsupported by the type of evidence they would demand in their own researches, is preferable to the inductive conclusions reached by scholars working objectively on the subjects involved. In doing so they merely show that a man may do excellent work in science without being a scientist at heart.

AMONG THE NUDISTS

By Frances and Mason Merrill

Alfred A. Knopf, Inc.

$3.00 5½ x 8; xviii + 247 *New York*

"Naked and unashamed" is the glad tidings conveyed by this pleasant piece of evangelistic writing. The authors quite evidently thoroughly enjoyed several weeks in a German nudist colony near Lübeck. Not content to let it go at that they then embarked upon a pious pilgrimage of nakedness, so to speak; imbibed the new gospel at the feet of the European masters, and then came home and wrote this book about it all. It is an entertaining treatise, at least in the descriptive portions which make up the bulk of the volume. The latter part, in which zeal to convey a Great Message and bring converts to the fold seduces its authors into trying to be philosophical and biological, did not amuse us. It is, in fact, as dull as a Christian Science tract.

Germany, it appears, is the Holy Land of nudism. Ecdysis is the order of the day, regardless of sex, age or previous condition of adiposity. In France the cult has hard sledding, and for a simple reason. The wicked and benighted Frenchmen make fun of the nudist apostles.

Doubtless no people enjoy the nude, in all its aspects, more than the French. But also no people have a keener perception of what is immediately ridiculous in an idea. And to tell them that they are unfair about it, or that health and hygiene should be considered, or to advance any earnest, soulful argument about something which they perceive to be composed of ridiculous elements, is only to make them yell with greater glee. God pity the Uplifter in France!

THE HISTORY OF THE MAYA. *From the Earliest Times to the Present Day.*
By Thomas Gann and J. Eric Thompson
Charles Scribner's Sons
$2.50 5¼ x 7¾; x + 264 *New York*

A history of the Mayan civilization must, in part, be more or less an outline. Nevertheless, the authors have written a book which will be of much interest to the general reader and useful as a reference book to the student. The chapters on the Origin of the Maya, history of the old empire, art and architecture, and the modern Maya have been contributed by Doctor Gann, leader of recent expeditions of the British Museum to Central America. Doctor Thompson, assistant curator of the Chicago Field Museum, has written the sections on the history of Yucatan, religion, religious ceremonies and traditions, daily life, warfare, food and clothing, and the calendar.

The volume is well illustrated, contains a bibliography of the more important references and is well indexed.

ILLITERACY IN THE UNITED STATES
By Sanford Winston
University of North Carolina Press
$3.00 5½ x 8½; xii + 168 *Chapel Hill*

A study, by partial correlation methods, of the relation between illiteracy and certain social phenomena, notably birth-rate, infant mortality, age at marriage, size of family, and suicide. In general, the correlations secured are about what would be expected; they show that decreasing illiteracy is associated with decreased birth-rate and infant mortality, with increased age at marriage, with decreased size of family, and with increased suicide. Whether illiteracy is causally related to any or all of these phenomena remains, of course, an open question.

MASTER MINDS OF MODERN SCIENCE
By T. C. Bridges and H. Hessell Tiltman
Lincoln Mac Veagh, The Dial Press
$3.00 5⅝ x 8⅜; 278 *New York*

A series of popular accounts of more or less prominent scientists and technologists. The fields of work represented are physics (8); engineering (5); agriculture, medicine, geology, chemistry, biology (2 each); astronomy and meteorology (1 each). (It might perhaps be fairer to transfer one paleontologist and one biochemist to biology.) The countries represented are England (17), the United States (2), and France, Germany, India, Italy, Poland, and Switzerland (1 each). It is perhaps fair to say that the authors expressly state that "our idea has been not merely to choose the greatest scientists of the present day, but rather to present as many different aspects of Science as possible, and to procure the material in each case from the one best able to give it."

OUTLINES OF AGRICULTURAL ECONOMICS. *Revised Edition*
By Henry C. Taylor *The Macmillan Co.*
$3.25 5¼ x 7¾; xii + 614 *New York*

"Better farm management, better mar-

keting, better land tenure, and a better distribution of wealth which will give the farmer a fairer share of the national income as a basis of a satisfactory life, and the nation a better agriculture and a better rural population as the basis of our national life, constitute the objective in the mind of the author of this volume. . . . . The book is intended to help toward an understanding of the principles which underlie the choice of a farm, the selection of crop and live-stock enterprises, the management of labor and equipment and the organization of these elements into an efficient going concern. Until these principles become a part of the thinking of the farmer and become a factor in guiding his actions, farming will lack efficiency. It is the action of the farmer himself that determines whether or not the farm is well managed."

A sound and useful volume, though most practical farmers of our acquaintance are too busy on the farm to read it.

AMONG THE ESKIMOS OF WALES, ALASKA 1890–93.
By Harrison R. Thornton. Edited and Annotated by Neda S. Thornton and William M. Thornton, Jr. *The Johns Hopkins Press*
$4.00 6¼ x 9¼; xxxviii + 235 *Baltimore*

An interesting and instructive account of the Alaskan Eskimos previous to the gold discoveries. The author lived for three years at Cape Prince of Wales. He describes the natives accurately and sympathetically.

THE INBORN FACTORS IN DISEASE.
An Essay
By Archibald E. Garrod
Oxford University Press
$2.75 (U. S. A.) *London and New York*
7s. 6d. net (England)
4¾ x 7¼; 160

A brief essay on the constitutional factor in disease, persuasively written by a physician of long experience. He argues for the ultimate chemical nature of individual differences:

> It might be claimed that what used to be spoken of as a diathesis is nothing else but chemical individuality. But to our chemical individualities are due our chemical *merits* as well as our chemical shortcomings; and it is more nearly true to say that the factors which confer upon us our predispositions to, and immunities from the various mishaps which are spoken of as diseases, are inherent in our very chemical structure; and even in the molecular groupings which confer upon us our individualities, and which went to the making of the chromosomes from which we sprang.

An interesting book for students of human constitution.

SOURCE BOOK IN ANTHROPOLOGY.
Revised Edition.
By A. L. Kroeber and T. T. Waterman
Harcourt, Brace and Co.
$3.00 5½ x 8½; viii + 571 *New York*

This new edition of a standard auxiliary text for courses in anthropology has been considerably altered in the revision. The selection of articles and passages for inclusion has been primarily based upon their utility in stimulating discussion. The 55 passages quoted are grouped under the following general heads: History of anthropology; evolution; heredity and race; prehistory; subsistence and material culture; social culture; aesthetic and religious culture; and dynamics of culture. The book is a valuable addition to the teachers' *armamentarium*, and is edited with sound critical judgment. There is a detailed index.

HUNGER AND LOVE
By Lionel Britton *Harper and Bros.*
$4.00 5¾ x 8⅜: x + 623 *New York*

The story of an English shop-boy's

struggle for existence and understanding of the universe.

DAS ANTLITZ DES ALTERS. *Photographische Bildnisse von Erich Retzlaff. Einleitung von Jakob Kneip*

Pädagogischer Verlag, G. m.b.H.
8.50 marks *Düsseldorf*
$8\frac{1}{4}$ x $11\frac{3}{4}$; 21 + 47 photographs

The viewpoint and the purpose of this beautiful volume are literary and artistic rather than scientific. The superb portraits of some 35 old men and women will, however, be of interest and use to students of human senescence, senility, and longevity. There is no index nor are the plates numbered.

THE FAMILY. *Source Materials for the Study of Family and Personality.*
By Edward B. Reuter and Jessie R. Runner

McGraw-Hill Book Co., Inc.
$4.00 $5\frac{3}{4}$ x 9; x + 615 *New York*

A source book which treats the adaptation of the family form to conditions in other times and places, the development of personality within the family group, and the adjustment of the family and its members to modern environment.

ANTHROPOLOGISCHE UNTERSUCHUNGEN IN ZÜRCHER KINDERGÄRTEN MIT BERÜCKSICHTIGUNG DER SOZIALEN SCHICHTUNG. *Inaugural-Dissertation zur Erlangung der philosophischen Doktorwürde vorgelegt der Philosophischen Fakultät II der Universität Zürich.*
By Bertha Niggli-Hürlimann

Art. Institut Orell Füssli
$6\frac{3}{4}$ x $9\frac{3}{4}$; 215 (paper) *Zurich*

The author bases her work on the measurements of 702 children aged 4 to 7 years. The children of the well-to-do classes are taller and heavier than those of the poor, and have broader shoulders, but do not differ from them in breadth of hips or chest circumference.

THE PROMOTION OF THE WELFARE AND HYGIENE OF MATERNITY AND INFANCY. *The Administration of the Act of Congress of November 23, 1921. Fiscal Year Ended June 30, 1929. United States Department of Labor, Children's Bureau Publication No. 203*

U. S. Government Printing Office
25 cents *Washington*
6 x $9\frac{1}{4}$; vi + 142 (paper)

This report is arranged under the following headings: Summary of state activities during 1929; Seven years' work of the cooperating states under the maternity and infancy act; Principal activities of individual states, 1929; Federal administration during 1929; and The services of the Children's Bureau under the maternity and infancy act. In a group of four appendices is given information on (a) the text of the act for the promotion of the welfare and hygiene of maternity and infancy and of supplementary legislation; (b) administrative agencies and officers; (c) infant and mortality rates; and (d) publications and exhibits of the Children's Bureau bearing upon maternal, infant, and child welfare and hygiene.

ZOOLOGY

A HISTORY OF ENTOMOLOGY
By E. O. Essig *The Macmillan Co.*
$10.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; vii + 1029 *New York*

A valuable contribution to the history of entomology. The author, professor of entomology at the University of Cali-

fornia and entomologist at the California Agricultural Experiment Station, has maintained essentially a western viewpoint throughout the treatise. With the rapid development of the West, particularly in agriculture and commerce, there has been an enormous development in entomological problems. These problems have received the attention of numerous investigators from the United States Division of Entomology, colleges and experiment stations. In order to trace the progress of these investigations and to preserve historical material which has been in danger of becoming more obscure as time goes on the author has written this book. The first eight chapters deal with the following subjects; Prehistoric entomology; California Indians in relation to entomology; historical background; principal institutions in California featuring entomology; some historical facts concerning the more important orchard mites and insects of California; the biological control of insect pests; insecticides; entomological legislation. Chapter IX includes nearly 300 pages and is devoted to biographical sketches. The author was unable because of lack of space to include many of those who have contributed to the development of entomology in California. His selection was as follows:

(1) some of the great founders of entomology whose influences are world-wide; (2) the fathers of entomology in North America, who established the science in this country and who described many western insects; and (3) the pioneer collectors, investigators, and teachers, who at some time worked within the confines of the state or described material taken here. In numerous instances these sketches are accompanied by photographs of individuals. Chapter X gives a chronological table showing the development and progress of entomology in relation to history and other sciences.

The work contains many figures and a number of tables. It is well documented and indexed.

A TEXTBOOK OF AGRICULTURAL ENTOMOLOGY

By Kenneth M. Smith *The Macmillan Co.*
$4.25 5½ x 8½; xiii + 285 *New York*

This book has been written for the advanced student, the agriculturist and the agricultural entomologist of the British Isles. While there is necessarily something of compilation in the book the author includes much original work. The elements of entomology have been omitted, since these are already adequately treated in a number of modern books. Insect pests of fruit have also been excluded, partly because of lack of space and partly because of the existence of a comprehensive book on them. The author, on the whole, has admirably succeeded in his aim to produce an up-to-date comprehensive treatise without being profuse. He has dealt with each insect in considerable detail, giving descriptions of the adult and its various stages and the main points in its life history. Control methods are given special attention. In each case the more important farm weeds which act as alternate hosts for many insects are given and also the natural enemies so far as these are known. The book is adequately illustrated and each chapter is well documented. There is an appendix on characteristic symptoms of insect attack, and on common farm weeds in relation to insect pests. In addition to the general index there are indices of authors and of parasites and predators.

THE BLOOD OF NORTH AMERICAN FRESH-WATER MUSSELS UNDER NORMAL AND ADVERSE CONDITIONS. *U. S. Department of Commerce, Bureau of Fisheries Document No. 1097.*
By M. M. Ellis, Amanda D. Merrick, and Marion D. Ellis

U. S. Government Printing Office
20 cents 7½ x 11; 34 (paper) *Washington*

Within recent years mussel beds of the upper Mississippi, which formerly were productive of shells on a commercial basis, have contained large numbers of dead and dying animals. This condition seems to have been produced by a change in the natural habitat of the mussel due to water contamination by municipal and industrial wastes, and navigation. In the fresh water mussels there is a very large volume of blood which, aside from its ordinary functions, is important in the locomotion of the animals. During activity, the foot expands to many times its retracted volume by an inflow of blood which can be retained there. When the foot is drawn within the shell the blood flows into numerous sinuses or reservoirs in various parts of the body.

This study of the physiological condition of the blood of twenty-seven species of North American fresh-water mussels shows it to be very low in solids as compared with the blood of other animals, both fresh water and marine. It is more alkaline than that of most animals. Although the blood contains only very small quantities of inorganic salts, these salts are balanced against each other as in higher animals. If the proportions or the quantities of these salts in the blood change within rather narrow limits, the activity of the heart and of the foot of the mussel ceases promptly. Mussels are very sensitive to changes in the salt content of the water in which they live. Because of their limited locomotion, changes in the water composition of their habitat produce within a few hours changes in the specific gravity and salt content of the blood.

Tables and charts in the paper exhibit the results of the various blood analyses. There is a bibliography.

NATURAL HISTORY OF THE BAY SCALLOP. *U. S. Department of Commerce, Bureau of Fisheries Document No. 1100.*
By James S. Gutsell
U. S. Government Printing Office
30 cents $7\frac{1}{2}$ x 11; 64 (paper) *Washington*

The bay scallop (*Pecten irradians*) is of considerable economic value, ranking third among American molluscs. Along the Atlantic Coast it ranges from Massachusetts to the Gulf of Mexico. Up to the present little has been known concerning its life history or its relation to its environment. This paper represents a comprehensive study of the natural history of the scallop. Particularly has the author studied in detail those phases which seemed to be of greatest importance in conservation. The work includes anatomical drawings and figures of developing embryos, growth curves, and charts showing the effect of varying salinity and temperature of the sea water upon mortality. There is a lengthy bibliography.

BIRD BANDING BY SYSTEMATIC TRAPPING. *Scientific Publications of the Cleveland Museum of Natural History, Vol. I, No. 5*
By S. Prentiss Baldwin
Cleveland Museum of Natural History
75 cents $6\frac{1}{4}$ x $9\frac{1}{4}$; 44 (paper) *Cleveland*

In this publication are reprints of two of the author's papers previously published elsewhere: *Bird banding by means of systematic trapping*, and *The marriage relations of the house wren.* The bird banding method discussed in the first paper was adopted by the U. S. Biological Survey in 1920 and the paper was issued as an instruction book on the subject. The author describes the methods of baiting and trapping in full, also a home record system

which is simple but effective. He includes examples of his findings. While it was possible for Mr. Baldwin to give only a limited amount of time to the work yet his results were surprising. How useful this method has been to the U. S. Biological Survey will be seen in the report which is made for the year 1930. During the year 1750 bird banders placed 182,263 bands and had return records on 10,000 banded birds.

In the second paper in this publication there is reported the results of records made on the mating of wrens and on incubation periods. The author has records on three generations of wrens in direct line, and numerous uncles, aunts, cousins, brothers and sisters. Apparently there is no inseparable bond between the mated birds. They have even been found to choose new mates for a second brood during the same season.

Both papers contain tabulations and record data. There are a number of illustrations.

ECOLOGICAL STUDIES OF THE BEET LEAF HOPPER. *United States Department of Agriculture Technical Bulletin No. 206*
By Walter Carter

U. S. Government Printing Office
30 cents 5¾ x 9; 115 (paper) *Washington*

A comprehensive study of *Eutettix tenellus* Baker, both in its native desert environment and in the beet field. It consists of an investigation of the relationships of the insect to its host plants and the relationships of the insect and the host plants to the desert, with its extreme physical factors of moisture and temperature. The possible explanation for the migration of the insect from the desert to the beet fields involves a study of all the factors of both environments which make for large *Eutettix* populations and their successful establishment in the beet fields. The fact that the insect transmits a virus which causes a disease of the beets necessitates the consideration of this disease, the insect's transmission of it, and the beet's susceptibility to it

Incorporated in the paper are numerous tables and diagrams exhibiting data collected on all the points studied. There is a bibliography of 32 titles.

BIRDS OF ARKANSAS. *University of Arkansas, College of Agriculture, Agricultural Experiment Station Bulletin No. 258.*
By W. J. Baerg

Agricultural Experiment Station
76 cents *Fayetteville, Ark.*
6 x 9; 197 (paper)

The chief value of this bulletin would seem to be in the information which it gives to the agriculturist concerning the economic value of birds, although teachers of nature study classes and bird lovers will find it a useful guide in field work in the Arkansas region. Three hundred and twelve species and sub-species are listed and described. Notes on the feeding and nesting habits, song and call notes, migration and other phases of bird life accompany the descriptions. No colored plates are included in the work and only 37 black and white illustrations. There are tables showing migration records, song period, and average song periods. The index contains both common and scientific names.

A MANUAL FOR THE STUDY OF INSECTS. *Revised Edition.*
By John H. Comstock, Anna B. Comstock and Glenn W. Herrick

The Comstock Publishing Co.
$4.00 6¼ x 9½; xiii + 401 *Ithaca, N. Y.*

At Professor Comstock's request Prof. Glenn W. Herrick took over the task of revising this book, which has already passed through eighteen editions since it first appeared in 1895. The aim of the author to make it more elementary has

been carried out by Professor Herrick. At the same time, in form and arrangement there has been little change. The subject matter has been brought up to date, but in order to meet the requirements of beginning courses in entomology the book has been simplified and condensed. While some of the old figures have been omitted, many new ones have been added.

This volume should be on the bookshelves of all biology laboratories. For teaching purposes it is invaluable. Even the layman who has some curiosity about insects will not find it too formidable. Once within its pages he will find much that is interesting and stimulating.

NATIONAL INSTITUTE OF HEALTH BULLETIN NO. 155. *1. Key Catalogue of Parasites Reported for Chiroptera (Bats) with Their Possible Public Health Importance, by C. W. Stiles and Mabelle O. Nolan. 2. The Confused Nomenclature of Nycteribia Latreille, 1796, and Spinturnix Heyden, 1826, by Benjamin J. Collins.*

U. S. Government Printing Office

30 cents *Washington*

5¾ x 9⅛; iv + 186 (paper)

Much careful work has gone into the preparation of these two papers, which will interest taxonomists chiefly. The public health importance of bats is not likely to be apparent at first thought, but it is discussed under six headings as follows: A. Bats as food; B. Bats as bloodsuckers; C. Bats as distributors of bedbugs; D. Bats as household pets; E. Bats as destroyers of mosquitoes; F. Bats as reservoirs of disease.

RELATIVE GROWTH AND MORTALITY OF THE PACIFIC RAZOR CLAM (SILIQUA PATULA, DIXON) AND THEIR BEARING ON THE COMMERCIAL FISHERY. *U. S. Department of Commerce, Bureau of Fisheries Document No. 1099.*

By F. W. Weymouth and H. C. McMillin

U. S. Government Printing Office

15 cents 7½ x 11; 24 (paper) *Washington*

This paper is one of a series of studies on molluscs of the Pacific Coast of North America. It deals with the relationships of the most abundant and only commercially important species, *Siliqua patula*. The variability, mortality, and sexual differences within the species are discussed. Data on the growth of clams from 10 localities are presented, together with a discussion of methods employed and localities considered. Similarities shown by the growth data and the conception of growth to which they lead is given, and a critical examination of the graphic representation and terminology follows. The differences exhibited by the various localities are discussed.

The authors include in their report tables of measurements and growth curves. There is a bibliography of 35 titles.

PADDLEWINGS. *The Penguin of Galápagos.*

By Wilfrid S. Bronson

The Macmillan Co.

$2.00 7½ x 8¼; 106 *New York*

An amusing book for young folks, particularly those to whom the New York Aquarium is accessible, wherein dwells the hero of this whimsical story. The author has spent many years at sea drawing and painting marine animals, and incidentally studying animal behavior. A good deal of natural history of the animals to be found in the region of the Galápagos Islands serves as the background for the thrilling experiences of this young penguin. The drawings will delight all intelligent children.

DEVELOPMENT AND LIFE HISTORY OF FOURTEEN TELEOSTEAN FISHES

AT BEAUFORT, N. C. *U. S. Department of Commerce, Bureau of Fisheries Document No. 1093.*
By Samuel F. Hildebrand and Louella E. Cable. *U. S. Government Printing Office*
35 cents 7½ x 11; 106 (paper) *Washington*

The teleosts which this paper deals with are as follows: *Anchoviella epsetus* (Bonnaterre) and *Anchoviella mitchilli* (Cuvier and Valenciennes), anchovies. *Orthopristis chrysopterus* (Linnæus), pigfish, hogfish. *Bairdiella chrysura* (Lacépède), white perch, sand perch. *Leiostomus xanthurus*, (Lacépède), spot. *Micropogon undulatus* (Linnæus), croaker, hardhead. *Parexocætus mesogaster* (Bloch), short-winged flyingfish. *Cypselurus furcatus* (Mitchell), four-winged flyingfish. *Decapterus punctatus* (Agassiz), scad, cigarfish, round robin. *Seriola dumerili* (Risso), amberfish, rudderfish. *Paralichthys dentatus* (Linnæus) and *Paralichthys albiguttus* (Jordan and Gilbert), summer flounder, southern flounder. *Symphurus plagiusa* (Linnæus), tongue-fish, sole. *Monacanthus hispidus* (Linnaeus), foolfish.

Numerous drawings illustrate the development of the various forms, and tables and curves show the rate of growth. There is a bibliography of fifteen titles.

PAPERS FROM TORTUGAS LABORATORY OF CARNEGIE INSTITUTION OF WASHINGTON. *Vol. XXVII. Carnegie Institution of Washington Publication No. 413*
Carnegie Institution of Washington
$7.00 (cloth) *Washington*
$6.00 (paper)
9 x 11⅝; 105 (paper)

This volume contains papers on *A cytological and biochemical study of the ovaries of the sea-urchin Echinometra lucunter*, by D. H. Tennent, M. S. Gardiner and D. E. Smith, in which the authors conclude that Golgi bodies and chondriosomes are not structural elements in the cellular architecture but the chemical products of physiological processes; *Observations on the formation of the egg of Echinometra lucunter*, by Ruth A. Miller and Helen B. Smith; *Studies on the coral reefs of Tutuila, American Samoa, with especial reference to the Alcyonaria*, by Lewis R. Cary; and *Formed components and fertilization in the egg of the sea-urchin Lytechinus variegatus*, by Esther C. Hendee.

COLLEGE ZOOLOGY. *Third Edition.*
By Robert W. Hegner *The Macmillan Co.*
$3.50 5½ x 8½; xxiii + 713 *New York*

In the revision of this standard textbook a chapter on Heredity and Genetics has been added but the general plan of the book, with its emphasis on function as well as on structure, has not been altered.

LABORATORY GUIDE FOR COLLEGE ZOOLOGY
By Robert W. Hegner *The Macmillan Co.*
$1.00 5½ x 8½; viii + 75 *New York*

This laboratory guide is designed for use with the author's *College Zoology*.

TRICHOMONAD FLAGELLATES FROM TERMITES. II. *Eutrichomastix, and the Subfamily Trichomonadinae. University of California Publications in Zoology Vol. 36, No. 10.*
By Harold Kirby, Jr.
University of California Press
$1.25 7 x 10¾; 92 (paper) *Berkeley*

SPECIES OF COCCIDIA IN CHICKENS AND QUAIL IN CALIFORNIA. *University of California Publications in Zoology, Vol. 36, No. 9.*
By Dora P. Henry
University of California Press
25 cents 7 x 10¾; 14 (paper) *Berkeley*

CRITICAL COMMENTS ON MAMMALS FROM UTAH, WITH DESCRIPTIONS OF NEW FORMS FROM UTAH, NEVADA AND WASHINGTON. *University of California Publications in Zoology Vol. 37, No. 1.*
By E. Raymond Hall
University of California Press
25 cents 7 x 10½; 13 (paper) *Berkeley*

THE MORPHOLOGY OF EUPOTERION PERNIX GEN. NOV., SP. NOV. *A Holotrichous Ciliate from the Intestine of Acmaea Persona Eschscholtz. University of California Publications in Zoology, Volume 36, No. 8.*
By Ronald F. MacLennan and Frank H. Connell *University of California Press*
25 cents 7 x 10½; 16 *Berkeley*

BOTANY

TAXONOMY OF THE FLOWERING PLANTS
By Arthur M. Johnson *The Century Co.*
$7.50 5¾ x 6⅝; xxi + 864 *New York*

This book is outstanding for its clearness and simplicity. The author, associate professor of botany in the University of California at Los Angeles, has had many years of teaching taxonomy. While intended for class-room use this volume will also be found useful by gardeners, horticulturists, foresters and nature lovers, and as a reference book for school and public libraries. The pen and ink drawings are a valuable feature of the book. These are numerous, well selected, and are executed with much skill. Quite aside from their illustrative value is the training which they give the student in acquiring a knowledge of what fundamental structures are of value in classification. Especial emphasis is placed by the author on the importance of diagrammatic and semi-diagrammatic drawings in making the study of taxonomy simple and effective.

The book is in two parts. The first nine chapters deal with the fundamental principles of flower analysis. The second part, also containing nine chapters, deals with systematics. There is a detailed and well arranged glossary. The bibliography contains many titles, also special sections on geological and paleontological references, ecology, history of botany, periodicals etc. There is an index for topics and one for figures. In spite of its 864 pages the book is not unduly heavy.

MAIZE IN SOUTH AFRICA
By A. R. Saunders
Central News Agency, Ltd.
20 shillings net *Johannesburg, South Africa*
5½ x 8½; 284

The total production of maize in South Africa is in general comparatively small. This is due in large part to geographic and climatic features and soil conditions. Nevertheless the author of this book shows how much can be done to offset these adverse conditions by proper selection of locality and seed, soil preparation, and after culture. Agriculturists in South Africa will find this treatise invaluable, while readers of general biological literature will find much in it that is interesting. The author is Senior Research Officer (Summer Cereals) of the Department of Agriculture of the Union of South Africa. After an introductory chapter on the history, origin, and importance of maize, he takes up in detail various phases of maize culture. There are chapters on statistics of production, climate in relation to maize production, soils, fertilizer practice and crop rotation, planting, cultivation, and harvesting. Considerable space is given to the botany of maize, the varieties, and

inheritance, breeding, and seed selection. There are also sections on diseases of maize and insect pests, the uses of maize, and maize in commerce.

The work concludes with a lengthy bibliography and an index.

PLANT PHYSIOLOGY. *With Reference to the Green Plant.*
By Edwin C. Miller
McGraw-Hill Book Company, Inc.
$7.00 5¾ x 9; xxiv + 900 *New York*

The author of this excellent textbook has had as a background for his work twenty years of teaching in the Kansas State Agricultural College, and the same number of years as plant physiologist in the Kansas Agricultural Experiment Station. His book has been designed for upper class men and graduate students. It will also be of value as a reference book in biological laboratories, both for students and investigators. Treating only of the physiology of green plants the author has incorporated into his book summaries of all the important researches of plant physiologists. The entire field is well and adequately covered. The arrangement of the material is excellent. An important feature of the book is the lengthy series of questions at the end of each chapter. To each chapter is also appended detailed reference lists. There are author and subject indices.

LIFE MOVEMENTS IN PLANTS. *Transactions of the Bose Research Institute, Calcutta, Vol. VI, 1930–1931.*
Edited by Sir Jagadis Chunder Bose
Longmans, Green and Co.
18s/net
$7.20 *London and New York*
5½ x 8¾; vi + 211

We have not found anything of momentous consequence in the present volume which will not be familiar to readers of Bose's previous works. The experiments described are interesting; but there is almost complete failure to notice the work and opinions of other investigators.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 353.* Containing following articles: *Methodik der Herstellung pflanzlicher Aschenbilder und Kieselskelette sowie von Anthrakogrammen*, and *Die Anfertigung von Dünnschliffen von rezenten pflanzlichen Materialien*, by Josef Kisser; *Die Schliffmethoden in der Paläobotanik*, by Karl A. Jurasky; *Die Mazerationsmethoden für rezente Pflanzengewebe*, by Josef Kisser; *Die Mazerationsmethoden in der Paläobotanik*, by Karl A. Jurasky; *Die kryoskopische Bestimmung des osmotischen Wertes bei Pflanzen*, by Heinrich Walter.
Urban und Schwarzenberg
10 marks 7 x 10; 179 (paper) *Berlin*

This number of the Abderhalden *Handbuch* is largely devoted to methods for the microscopic examination of plant tissues.

KEIMUNGSPHYSIOLOGIE DER GRÄSER (GRAMINEEN). *Eine Lebensgeschichte des reifenden, ruhenden und keimenden Grassamens.*
By Ernst Lehmann and Fritz Aichele
Ferdinand Enke
60 marks (paper) *Stuttgart*
63 marks (cloth) 6½ x 10; xxiii + 678

The questions involved in the development and sprouting of seeds are of great theoretical and practical importance. In this voluminous work the authors synthesize the present knowledge of this field for the cereals. There is a bibliography of 75 pages and an index.

SOME FAMILIAR WILD FLOWERS
By James E. Jones *The Macmillan Co.*
$1.50 4¾ x 7½; 90 *New York*

A pocket guide containing excellent photographs with brief descriptions.

MORPHOLOGY

CONCERNING, *Earliest First Growth in the Human Ovum; Origin of First Blood Corpuscle and Plasm—First Blood Space and Vessel—The Three Blood Circulations—Blood Corpuscle Differentiation from First Multinucleolated Uncolored Nucleus-Blood-Corpuscle to the Final Non-Nucleated Red Blood Corpuscle of Maturity—the Erythrocyte—the Red Blood Plastid of Minot—Origin of the Cancer.*
By Frank A. Stahl *Frank A. Stahl*
6 x 9¼; 157 *Hamilton Club, Chicago*

The gist of Dr. Stahl's doctrine is as follows:

"This search for the First Blood Corpuscle; its rapid differential proliferation; division, multiplication, etc., naturally stirred up relative queries.

"In the one case the primal syncytial nucleus-cellule gives rise to the first blood corpuscle. Its polynucleoli render fierce and rapid multiplication and differentiation, to the and forming the blood corpuscles of the first or primal blood circulation.

"In another direction this syncytial proliferation develops the pseudodecidua in the placentation of the extrauterine pregnancy; as is well known this function is autogenous in the uterine pregnancy.

"Here are two differing expressions and unequal in spread and substance, yet carefully limited in both spread and substance, in these two distinct and separate loci of placentation and pregnancy. How explain this unequal development in position, spread and substance?

"Both are under a normal growth control ion or hormone principle. And as is well known, there where this control lags or is decreased there the benign placental polyp; this at times going on to malignant expression. Why, because of loss or lack of this normal growth control ion over proliferation."

ANATOMIE UND PATHOLOGIE DER SPONTANERKRANKUNGEN DER KLEINEN LABORATORIUMSTIERE. *Kaninchen. Meerschweinchen. Ratte. Maus.*
By H. J. Arndt, C. Benda, J. Berberich, J. Fiebiger, E. Flaum, E. Haam, F. Heim, A. Hemmert-Halswick, E. Hieronymi, R. Jaffé, W. Kolmer, A. Lauche, E. Lauda, W. Lenkeit, K. Löwenthal, R. Nussbaum, B. Ostertag, E. Petri, E. Preissecker, L. Rabinowitsch-Kempner, P. Radt, Ph. Rezek, W. Rohrschneider, H. Schlossberger, Ph. Schwartz, O. Seifried, R. Weber, W. Worms. Edited by Rudolf Jaffé.
Julius Springer
98 marks (paper) *Berlin*
6½ x 9⅝; xix + 832
102 marks (bound)

This book on the normal and pathological anatomy of rabbits, guinea pigs, rats, and mice, is intended to help the experimenter in deciding whether the results which he observes were caused by his experimental procedure or by a spontaneous illness of the animal. It is an extremely valuable addition to the working reference literature of biology and experimental medicine.

ERKENNTNIS *zugleich Annalen der Philosophie Band IX, Heft 5, im Auftrage der Gesellschaft für empirische Philosophie Berlin und des Vereins Ernst Mach in Wien. Band I, Heft 5.*
Edited by Rudolf Carnap and Hans Reichenbach *Felix Meiner*
4 marks 6¼ x 9¼; 80 (paper) *Leipzig*

The present number of this philosophical journal contains articles by Friedrich Kraus on *The Problem of Unity and Multiplicity from the Biological Standpoint*, and by Ludwig von Bertalanffy on *Facts and Theories of Morphogenesis as an Approach to the*

Problem of Life. The latter is of first rate importance.

VEINS IN THE ROOF OF THE BUCCO-PHARYNGEAL CAVITY OF SQUALUS SUCKLII. *University of California Publications in Zoology, Vol. 37, No. 3.*
By J. Frank Daniel and L. H. Bennett
University of California Press
25 cents *Berkeley*
7 x 10¾; 6 (paper)

FEATURES IN THE DEVELOPMENT OF AMMOCOETES. *University of California Publications in Zoology, Vol. 37, No.4*
By J. Frank Daniel
University of California Press
25 cents 7 x 10¾; 12 (paper) *Berkeley*

PHYSIOLOGY AND PATHOLOGY

ADVENTURES IN BIOPHYSICS
By A. V. Hill
University of Pennsylvania Press
$3.00 6 x 9; ix + 162 *Philadephia*

There are few scientists who can write more interestingly of difficult subjects than A. V. Hill. The present volume is no exception. It consists of five lectures given before the Johnson Foundation for Medical Physics. The subjects are: Some adventures with vapour pressure; the state of water in tissues; the conception of the steady state; the time-relations of events in muscular contraction; the mechanics of muscular contraction and other matters.

LE DOSAGE DES SELS BILIAIRES DANS LA BILE ET LE LIQUIDE DUODÉNAL
By Louis Cuny *Masson et Cie*
30 francs 6⅜ x 9¾; 222 (paper) *Paris*

This appears to be an excellent study of the problem of measuring quantitatively the excretion of bile salts. The literature from every land has been well gone over and the authors have made a number of contributions besides. There is a fine bibliography.

The book should be in the hands of everyone who is interested in this difficult problem.

THE PATHOLOGY OF INTERNAL DISEASES
By William Boyd *Lea and Febiger*
$10.00 net 5¾ x 9¼; 888 *Philadelphia*

This book not only treats the pathological anatomy, and in many cases the pathological physiology, of internal diseases but correlates them with clinical symptoms. It is excellently illustrated and contains bibliographies and an index.

LA PRESSION VEINEUSE PÉRIPHÉRIQUE. *Étude Physiologique, Clinique et Thérapeutique*
By Maurice Villaret, Fr. Saint Girons and L. Justin-Besançon. *Masson et Cie*
38 francs 6¼ x 9½; 318 (paper) *Paris*

We have here a satisfactory and useful review of what work has been done so far on venous pressure in health and disease. Unfortunately the study of this subject does not, as yet, seem to have been of much help to the physician who is attempting to diagnose and treat diseases of the circulatory system.

There is a good bibliography, in which workers foreign to France are well represented. The index is satisfactory. The work should be in the library of everyone who is interested in this subject.

LE GLYCOGÈNE *dans le Développement des Tumeurs des Tissus Normaux et des Êtres Or-*

ganisés. Physiologie Normale et Pathologique.

By A. Brault *Masson et Cie*

80 francs 6½ x 10; 367 (paper) *Paris*

The researches which are recorded in this book led Dr. Brault from the occurrence of glycogen in cancers to its rôle in the normal development of different organisms, including the invertebrates and protozoa. He concludes that "glycogenesis is a universal function inherent in the very constitution of the protoplasm and completely independent from one organ to another."

LEHRBUCH DER ALLGEMEINEN PHYSIOLOGIE.

With the collaboration of L. Asher, W. von Buddenbrock, E. Gellhorn, C. Oppenheimer, J. Spek. Edited by Ernst Gellhorn

Georg Thieme

47 marks (paper) *Leipzig*

49.50 marks (cloth)

6¾ x 10; xiii + 741

This book deals with the physical and chemical processes which condition vital phenomena. The topics treated are as follows: the cell as a physico-chemical system; chemistry of the cell processes; energetics of living substance; the cell as a morphological system; general physiology of development and morphogenesis; general physiology of stimulation; tropisms. There are bibliographies for each section, and an index.

BIOCHEMISTRY

KOSTYCHEV'S CHEMICAL PLANT PHYSIOLOGY. *Authorized Edition in English with Editorial Notes.*

By S. Kostychev (Translated and edited by Charles J. Lyon) P. Blakiston's Son and Co., Inc.

$6.00 net 6 x 9⅛; xv + 497 *Philadelphia*

A translation, revised and brought down to date by the author, of a volume which appeared in German in 1926. There are chapters on: The foundations of chemical plant physiology; the assimilation of solar energy by green plants and the primary synthesis of organic compounds; chemosynthesis and the assimilation of molecular nitrogen; plant nutrition with prepared organic compounds; the mineral nutrition of plants; carbohydrates and proteins; the transformations of these substances in the plant; secondary plant substances; respiration and fermentation.

The book will be a useful one to English speaking students.

SEX

IDEAL MARRIAGE. *Its Physiology and Technique*

By Th. H. Van de Velde. Translated by Stella Browne. *Covici, Friede, Inc.*

$7.50 *New York*

5⅜ x 8½; xxvi + 323 + 7 plates

This book is a detailed manual of the technique of the art and mystery of human copulation. When we say this we mean it. Nothing is left either out or to the imagination. It is precise, detailed, and scientifically accurate on every *minutia* of the business to which it addresses itself. It is a pedantically humorless treatise about a subject, which many wiser men than its author long ago perceived to be essentially as ridiculous as it is pleasant and biologically necessary.

Naturally such a book is well suited to a civilization so little subtle as ours today is. It has had a great sale in its original German dress. There is every reason to suppose that this English translation will be equally successful. Reginald the Office Boy has already sent off three copies as wedding presents; but, with that sagacity

far beyond his years which he occasionally displays, says he believes that the greatest sphere of usefulness of this book will be in our coeducational institutions.

Theoretically the sale of the book is "positively restricted to physicians, lawyers, ministers, educators and social workers." Anyone, if there should be anyone, not coming within these categories when constructively interpreted, may take comfort in the thought that the 18th amendment to the constitution theoretically restricts the sale of alcoholic beverages.

BIOMETRY

CORRELATION ALINEMENT CHARTS IN FOREST RESEARCH. *A Method of Solving Problems in Curvilinear Multiple Correlation. U. S. Department of Agriculture Technical Bulletin No. 210.*
By Donald Bruce and L. H. Reineke
U. S. Government Printing Office
15 cents $5\frac{3}{4}$ x 9; 88 (paper) *Washington*

A development of the theory of correlation, partially graphic in its technique, which has a wide applicability to forestry problems, many of which have hitherto seemed insoluble. So technical a subject cannot be adequately discussed briefly, but its importance can be indicated by listing some of the problems to which it can be applied successfully. Among these are: decomposing dextrose by sulphuric acid at high temperatures; bark thickness; damping-off of coniferous seedlings in which the variables have a periodic character; cell-sap density or osmotic pressure with site quality; soil and air temperatures; soil moisture; relation of resin flow to size and age of tree and to climatic factors; viability of seed, as affected by size, weight, age and storage temperatures. In nursery practice, size of plants may be related to amount of fertilizer or other chemicals, amount of water and growing space. Skidding time, or cost, in logging studies may be correlated with log diameter, length, and skidding distance, or sawing time in the mill may be correlated with size, amount of defect, etc. In pulp and paper investigations, yields or breaking strength may be related to composition of liquor, temperature, pressure, duration of cook, percentages of species or types of pulp, etc.

Included in the paper are numerous tables and figures exhibiting regression lines, curves, alinement charts, etc. In an appendix will be found short cut methods in handling the statistical material. There is a bibliography of 48 titles.

AN INTRODUCTION TO MEDICAL STATISTICS
By Hilda M. Woods and William T. Russell
P. S. King and Son, Ltd.
7s. 6d. net $4\frac{3}{4}$ x $7\frac{1}{8}$; x + 125 *London*

This little book was prepared as a text for students taking the course for the Diploma in Public Health in the London School of Hygiene and Tropical Medicine. In little more than a hundred pages it gives a considerable amount of information on the sources of vital statistics—the census and registration of births, deaths, and sickness—on tabulation of data, graphs, population estimates, birth and death rates, standardized rates, averages, measures of dispersion, correlation and regression, life tables, and sampling. Though the student who masters it will not yet be an expert statistician, he will have had a sound introduction to medical statistics, and the authors hope that this will whet his appetite for more.

STATISTICAL TABLES AND GRAPHS
By Bruce D. Mudgett
Houghton Mifflin Co.
$1.75 5 x $7\frac{1}{2}$; viii + 194 *Boston*

This book is designed "not for the students who intend later to become statisticians, but rather for those who intend to become business men, and emphasis has been placed on those elementary statistical methods with which business men are likely to come into most intimate contact." The matter is sound and well presented. In spite of the author's disclaimer we feel that statisticians, as well as business men, will profit by reading the book.

AN ELEMENTARY TREATISE ON ACTUARIAL MATHEMATICS

By Harry Freeman *The Macmillan Co.*
$8.50 5½ x 8½; xiii + 399 *New York*

A well-written textbook, which should be of some value to others than prospective actuaries. The subjects treated, and the space allotted, are as follows: trigonometry, 21 pages; finite differences and interpolation, 112 pages; functions and limits, 17 pages; differential calculus, 73 pages; integral calculus, 91 pages; and probability, 57 pages. There is an extended collection of problems.

THE SMOOTHING OF TIME SERIES

By Frederick R. Macauley

National Bureau of Economic Research, Inc.
$2.00 6 x 9; 172 *New York*

A study of various methods of smoothing, with extensive illustrations, which will be useful to anyone who has to deal with time series. We should have liked, however, to have had included a discussion of the broader aspects of the problem; in particular, as to when smoothing is justified, as to how much labor is warranted, and as to the meaning to be attached to differences in results obtained by different methods of smoothing.

SOME RECENT RESEARCHES IN THE THEORY OF STATISTICS AND ACTUARIAL SCIENCE

By J. F. Steffensen *The Macmillan Co.*
$2.00 5½ x 8½; vii + 48 *New York*

Three lectures on various points of statistical and actuarial theory. Of particular interest are the discussion of presumptive values of frequency constants and of the theoretical foundations of the Pearsonian and the Gram-Charlier frequency curves. The author objects to presumptive values, on the ground that their use leads to theoretical contradictions; and he expresses the opinion that the Pearsonian curves are of more general utility than the various series expansions.

PSYCHOLOGY AND BEHAVIOR

BRAIN AND PERSONALITY. *Studies in the Psychological Aspects of Cerebral Neuropathology and the Neuropsychiatric Aspect of the Motility of Schizophrenics*

By Paul Schilder

Nervous and Mental Disease Publishing Co.
$3.00 *Washington and New York*
6 x 9; v + 136

This series of lectures deals with problems of consciousness; problems of tonus; encephalitis; optic agnosia; speech disturbances; the postural model of the body; psychic and organic apparatus; actual causes and regression in neurosis and psychosis; transference in schizophrenia; impulse, postural and righting reflexes in relation to hyperkinetic states; akinetic states, stupor and negativism; mannerisms and emotions; catalepsy, motor troubles and personality. The author finds that organic lesions as well as psychic disturbances produce a regression to more primitive levels of behavior. The following bit of Lamarckianism amused us:

"We wish to mechanize what once had a real meaning. In that way, by the way, we can understand the genesis of organs of the organism. The organism produces tools in order not to be compelled again and again to a psychic effort."

THE ISLAND OF PENGUINS
By Cherry Kearton

Robert M. McBride and Co.
$3.00 5½ x 8½; 248 *New York*

Because the book contains so much that is interesting in its text and particularly its numerous and excellent photographs the reader is the more irritated by its defects. These are of two sorts: First, a vagueness and lack of precision regarding simple points which finally make one dubious about the trustworthiness of anything in the book; and, second, the persistent attribution to the penguins of the same psychological motives, feelings and emotions that are in human beings associated with behavior objectively more or less like that observed among the penguins. Illustrative of the first point is the failure of the author to reveal the name or location of the island upon which he made his observations. It is vaguely said to be a small island with a lighthouse on it somewhere northwest of Capetown. As to the length of time Mr. Kearton stayed there the reader may take his choice among "many months" "several weeks," and "five months." On the second point it is obviously not only permissible but interesting and desirable to point out all possible objective similarities between the behavior of penguins and of men, but talk about she-penguins being "drowsily meditating on the perfect bliss of married life," or he-penguins "giving advice," or both of them being "house-proud," when it is continued for page after page throughout the book is not only unwarranted but finally becomes nauseating.

Altogether it is a pity that the author made such poor use of a remarkable opportunity. The illustrations, as has been said, are mainly excellent. They are the chief recommendation of the book, which lacks an index.

WHOLE AND PART METHODS IN TRIAL AND ERROR LEARNING. *Comparative Psychology Monographs, Vol. 7, No. 5, Serial No. 35.*
By Ella May Hanawalt

The Johns Hopkins Press
$1.25 6⅞ x 10; 65 (paper) *Baltimore*

In the introduction to this paper the author gives an historical review of the work done on evaluating the experimental methods in the psychology of learning. She sums up the advantages and objections of the whole method and the part method which have been suggested or indicated by various investigators. A review of the experiments by Pechstein on white rats is given. The present study developed out of this line of work. The investigations were done in the psychological laboratories at the University of Michigan. The maze was the type designated as the "Shepard universal type." Fifteen male albino rats were used.

"The whole method proved to be superior to either the pure part, progressive part, reversed repetitive part, modified reversed repetitive part, or direct repetitive part methods for rats in learning maze patterns.

"Practice on parts and on part combinations before running the whole contributed to learning, but did not save enough to compensate for the extra energy required.

"Some important factors in causing waste in part learning were

"a. Breaking up the unity of the total pattern.
"b. Increasing the number of separate learning acts.
"c. Learning in a direction opposite to that in which the learning must ultimately function.

"Compatibility of parts learned as parts when required to function with other parts or with the whole

was not immediate, but required practice of the part in its new relationship.

"Trained learners did not acquire increasing facility in learning problems of similar type and of comparable difficulty. They had attained a considerable uniformity of performance.

"The mastery of one part did not affect either positively or negatively the mastery of others when the problems were unique in character.

"The influence of distribution of repetitions on amount of energy required for learning for immediate recall is in need of further experimental study.

"Individual differences among learners is a probable factor in learning efficiency regardless of method employed."

Included in the paper are tables and figures. There is a bibliography of 31 titles.

YOUR COMPLETE LIFE
By Walter J. Bankes
The Christopher Publishing House
$1.25 5¼ x 7¾; 74 *Boston*

"For many years it has been my deep conviction that the principles of psychology should be expressed by someone in such simple language that anyone may interpret and apply their meaning to the various periods of development in life."

We cannot say that the result of this conviction, as expressed in the book before us, has seemed of great importance.

CONDITIONED EYELID REACTIONS TO A LIGHT STIMULUS BASED ON THE REFLEX WINK TO SOUNDS. *Psychological Monographs, Vol. XLI, No. 1, Whole No. 184.*
By Ernest R. Hilgard
Psychological Review Co.
75 cents *Princeton, N. J., and Albany, N. Y.* 6¾ x 9¾; v + 50 (paper)

An interesting paper, not easily reviewed within a limited space. The investigator selected the eyelid reaction because "it involves a very light and mobile bodily member lending itself to a study of the controls which operate in the intact individual affecting relatively simple muscular activity. Involuntary blinking occurs more or less throughout the waking hours, and there is some measure of deliberate or voluntary control over the eyelid in opening or closing the eye. This interplay of reflex and voluntary action points to a probable significance of the eyelid reaction in an experimental program dealing with the modifiability of human behavior."

"Conditioned eyelid reactions were obtained from five out of eight subjects after successive presentations of a light stimulus preceding a sound stimulus by 200σ to 400σ. The Dodge pendulum-photochronograph was used as the basic instrument for presenting the stimuli and for recording the stimuli and reactions photographically. . . . The light stimulus evoked at the start only occasional minimal unconditioned reflexes of a latency lower than that of the conditioned responses which later developed. The conditioned reaction appeared during the series of paired light and sound presentations as the initial component of a dual or dicrotic response, anticipatory to the second component which was the unconditioned reflex to sound. The isolated presentation of the light after such a series elicited a wink homologous with the first component of the dual response.

"The limited experimentation on conditioning as a learning process and the theoretical objections which may be raised against considering the conditioned reaction to be the unit of habit, suggest that for the present it may be better to think of conditioning as a sample of learning rather than as the foundation for learning theory."

Included in the paper are graphs and tables. There is a bibliography of 50 titles.

ANIMAL MOTIVATION. *Experimental Studies on The Albino Rat*
By C. J. Warden. With the Collaboration of T. N. Jenkins, L. H. Warner, Marion Jenkins, E. L. Hamilton and H. W. Nissen
Columbia University Press
$5.00 5⅝ x 8¾; xii + 502 *New York*

An account of studies on various drives —hunger, thirst, sex, maternal, and exploratory—in the albino rat, carried on by a uniform technique, the obstruction method. This consists essentially in

requiring the animal to undergo a disagreeable experience (in this case, an electric shock) in order to reach a desired object—food, water, etc. The volume is an important contribution to comparative psychology.

THE MEANING OF PSYCHOANALYSIS
By Martin W. Peck
Alfred A. Knopf, Inc.
$2.50 5 x 7½; xix + 273 *New York*

AMERICAN TYPES. *A Preface to Analytic Psychology*
By James Oppenheim *Alfred A. Knopf, Inc.*
$2.50 5 x 7½; 210 *New York*

These two books, by American disciples of Freud and Jung, are popular introductions to their subjects. Peck's book, based on lectures given in the Harvard Medical School, is distinctly the better written book. Oppenheim's attempt to expound Jung's psychology of types suffers, we feel, from a style unsuited to a reasoned scientific discussion. We cannot say that either book has brought us measurably nearer a complete acceptance of either theory.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A PRAGMATIST THEORY OF TRUTH AND REALITY
By Samuel S. S. Browne
Princeton University Press
$2.00 6 x 9; 95 *Princeton*

We suggest that the following passage be read aloud:

> The important point to understand is that A's being B does not imply that A has inhering in it a universal quality called B or B-ness. A can be B when it is not known, but B cannot be B when it is not known, for B is a universal constructed by thought. B cannot be at all except in the knower's mind. Nevertheless, A can be B previous to its being known, for it is not necessary that B shall have become B in order that A shall become B. A's becoming B is ontological, but B's becoming B is epistemological. When A became B, an historical event occurred on which depends the applicability of B, when conceived, to A. This may be otherwise expressed by saying that particulars exist independently of thought, but universals do not. B is a universal, although there may be but one object in the Universe to which it can be applied. We cannot deny that A was B apart from thought if this denial is understood to mean that A was C instead of B, but we must deny it in the sense that B subsisted *qua* a universal inhering in A. If A-in-itself were really C, then C would be a universal and would have to be known; and having thus spoiled the truth of the conception that A is B, which we are not allowed to do *ex hypothesi*, we would be left with the same problem as before. Hence, A was not C; it was B; but it did not have B inhering in it as a quality. A's being B implies simply that when I conceive A, I conceive it to be B, and my conception is true.
>
> "Of course, since the B-ness of A is my conception, so also is the A-ness of A. For A, although in one sense a particular existent independent of me, is also, in another sense, a universal conceived by me and hence having no being beyond my thought. In recognizing A as A, I am subsuming the particular A under the universal A. I am making A A epistemologically. It is not A until I have done so. It may be a chaos, but more probably it is not an *it* at all.
>
> "Consequently we have no right to say that A is A wholly apart from thought, although we are justified in saying that it was A temporally previous to thought. This temporal previousness is itself part of my conception."

REASON AND NATURE. *An Essay on the Meaning of Scientific Method.*
By Morris R. Cohen
Harcourt, Brace and Co.
$5.00 6 x 9; xxiv + 470 *New York*

A work which has taken Professor Cohen twenty years to write cannot profitably be reviewed in half a dozen lines. We can, however, heartily recommend our readers to try it for themselves, assuring them that they will find both pleasure and profit in it.

Professor Cohen has assisted the reviewer in the following paragraphs from his preface:

"To readers who have a predilection for conventional labels, I offer the following:

"I am a rationalist in believing that reason is a genuine and significant phase of nature; but I am an irrationalist in insisting that nature contains more than reason. I am a mystic in holding that all words point to a realm of being deeper and wider than the words themselves. But I reject as vicious obscuratism all efforts to describe the indescribable. I reject the euthanasia or suicide of thought involved in all monisms which identify the whole totality of things with matter, mind, or any other element in it. But I also reject the common dualism which conceives *the* mind and *the* external world as confronting each other like two mutually exclusive spatial bodies. I believe in the Aristotelian distinction between matter and form. But I am willing to be called a materialist if that means one who disbelieves in disembodied spirits; and I should refer to spiritists who localize disembodied spirits in space as cryptomaterialists. However, I should also call myself an idealist, not in the perverse modern sense which applies that term to nominalists like Berkeley who reject real ideas, but in the Platonic sense according to which ideas, ideals, or abstract universals are the conditions of real existence, and not mere fictions of the human mind.

"To those who labour under the necessity of passing judgment on this book in terms of current values, I suggest the following:

"The author seems out of touch with everything modern and useful, and yet makes no whole-hearted plea for the old. He believes in chance and spontaneity in physics and law and mechanism in life. He has no respect for *experience*, *induction*, *the dynamic*, *evolution*, *progress*, *behaviorism*, and *psychoanalysis*, and does not line up with either the orthodox or revolutionary party in politics, morals, or religion, though he writes on these themes. He offers no practical message to the man engaged in the affairs of life, and seems to be satisfied with purely contemplative surveys of existence."

THE HISTORY OF SCIENCE AND THE NEW HUMANISM

By George Sarton *Henry Holt and Co.*

$2.00 5 x 7⅞; 178 *New York*

The New Humanism praised by Sarton in this book is a very different kind of humanism from that which created quite a stir a couple of years ago. Sarton's humanism is to be built around science, but is to include much more.

The New Humanism will not exclude science but on the contrary exploit it to the utmost; it will minimize the danger of scientific knowledge abandoned to its own technicalities; it will extol the human implications of science, and reintegrate it into life; it will bring together into a single communion scientists, philosophers, artists and saints. It will confirm the one-ness of mankind, not only in its achievements but in its aspirations. The evils of the so-called "machine age" have been caused by the aloofness of the old humanists as well as by the narrowmindedness of some scientists, but above all by the insatiable greed of men of prey. This "machine age" must go, and be replaced at last by the "scientific age;" we must prepare a new culture, the first to be deliberately based upon science, upon humanized science,—the New Humanism.

We can recommend the book unreservedly to the attention of our readers.

SIR D'ARCY POWER: *Selected Writings 1877–1930.*

Oxford University Press

$9.50 5½ x 9; x + 368 *New York*

This is a delightful collection of historical essays by a distinguished British surgeon and historian of medicine. While mainly upon medical and surgical topics, the biologist will find much to interest him. It appears that Samuel Pepys' eye trouble, which caused him to give up his shorthand diary, would probably have been completely relieved by spectacles of the following prescription

+ 2 D. c. + 0.50 D. cyl. axis 90°

but nothing could be done for him in his day because nobody knew anything about astigmatism.

There is a good deal of interesting matter in this volume about John Hunter, William Harvey, and various other lesser lights. At the end is a short-title bibli-

ography of D'Arcy Power's writings to date. It includes 609 titles. There is an excellent index.

THE LOGIC OF SCIENCE
By Harold R. Smart
D. Appleton and Co.
$2.50 5¼ x 8; vii + 237 *New York*

A discussion of the nature of science and the logical and philosophical problems involved. On the whole, the discussion of mathematics and physics seems to us somewhat better done and more valuable than the discussion of the biological sciences.

FOUNDATIONS OF SCIENCE
By Garfield A. Bowden
P. Blakiston's Son and Co., Inc.
$1.68 5¼ x 7½; x + 753 *Philadelphia*

This textbook of general science for junior high schools is more interestingly written than most of its class.

SCIENCE AND FIRST PRINCIPLES.
By F. S. C. Northrop *The Macmillan Co.*
$3.00 5¾ x 8½; xiv + 299 *New York*

We refuse to express an opinion as to the merits of the cosmological theory offered in this book. That may be left to experts. The discussion of physical principles and the author's account of the history of science are well worth reading for their own sake.

NOVIUS ORGANUM. *Essays in a New Metaphysic*
By James C. McKerrow
Longmans Green and Co.
$3.00 5½ x 7¾; viii + 277 *New York*

A collection of papers attempting to answer various philosophical, biological, economic, and moral questions. Some of the author's speculations are entertaining, but we have found most of them hardly convincing.

THE COST OF BIOLOGICAL BOOKS IN 1931

By JOHN R. MINER

Department of Biology, School of Hygiene and Public Health, Johns Hopkins University

IN ACCORDANCE with the usual custom of THE QUARTERLY REVIEW OF BIOLOGY, the present paper reports on the cost of the books which have been received during 1931. The books are classified by origin in the same rubrics as in previous reports.

The total number of pages reviewed in 1931 is 121,179, an increase of 8.9 per cent over 1930 and of 46.8 per cent over 1926. As in every previous year except 1928 the English-American books are the most expensive. However, these prices include both transportation and the United States tariff, whereas the prices for other groups, being for the country of publication, do not include either of these charges.

German books, which in every previous year had shown an increase in cost, in 1931 declined 3.8 per cent from 1930. They are still, however, well above the cost of any other group except the English-American.

Books published in the United States show a general downward trend in cost over the six years and are now 6.3 per cent below 1926. As these are the books most used by American biologists, this is an auspicious phenomenon for the latter.

French books, which increased abruptly in price in 1928, have again in 1931 increased 46.8 per cent over 1930, so that

TABLE 1

Prices of biological books, 1931

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
English-American	8,516	$193.30	2.27
German	10,323	180.26	1.75
Other Countries	1,970	30.11	1.53
England	2,742	32.68	1.19
United States	85,682	898.59	1.05
British Government	366	3.76	1.03
France	8,148	55.96	0.69
U. S. Government	3,432	9.51	0.28

TABLE 2

Comparison of the prices of biological books from 1926 to 1931

ORIGIN	AVERAGE PRICE PER PAGE						CHANGE + OR − FROM 1930 TO 1931		CHANGE + OR − FROM 1926 TO 1931	
	1926	1927	1928	1929	1930	1931	Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
English-American	1.55	1.39	1.46	1.90	1.91	2.27	+0.36	+18.8	+0.72	+46.5
Other countries	1.51	0.78	1.13*	1.68	0.97	1.53	+0.56	+57.7	+0.02	+ 1.3
England	1.28	1.14	1.09	1.29	1.13	1.19	+0.06	+ 5.3	−0.09	− 7.0
United States	1.12	1.09	1.14	1.14	1.09	1.05	−0.04	− 3.7	−0.07	− 6.3
Germany	1.09	1.20	1.48	1.65	1.82	1.75	−0.07	− 3.8	+0.66	+60.6
British Government	—	0.96	1.26	0.39	1.19	1.03	−0.16	−13.4	+0.07†	+ 7.3†
France	0.35	0.36	0.45	0.47	0.47	0.69	+0.22	+46.8	+0.34	+97.1
U. S. Government	0.31	0.24	0.21	0.23	0.30	0.28	−0.01	− 6.7	−0.03	− 9.7

* With two special treatises omitted as explained in Vol. III, p. 601.

† Change from 1927 to 1931.

their price is now nearly double that of 1926. They are still, however, only about two-thirds as expensive as any other group of commercially produced scientific books. The biological books published by the United States Government are, as usual, at the bottom of the list.

Combining all books reviewed in 1931 the average price per page was 1.159 cents, an increase of 2.5 per cent as compared with 1930, and of 5.7 per cent as compared with 1926. There has been no marked change in the general price level of the books reviewed.

It should be remembered that these reports are based on small samples of books in general and, for some countries, on small samples of the biological books published. The reader should, therefore, be mindful of the dangers of applying conclusions from samples to the general domain of book prices.

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